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The Marine Benthic Algal Flora of Puerto Rico, IIIA. Rhodophyta Excluding Rhodymeniales and Ceramiales

David L. Ballantine,
James N. Norris,
and
Hector Ruiz

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ABSTRACT

Ballantine, David L., James N. Norris, and Hector Ruiz. *The Marine Benthic Algal Flora of Puerto Rico, IIIA. Rhodophyta Excluding Rhodymeniales and Ceramiales*. Smithsonian Contributions to Botany, number 121, x + 182 pages, 136 figures, 2025.—This account is a taxonomic study of the benthic red algal species (except the Rhodymeniales and Ceramiales) from Puerto Rico, Caribbean Sea. In this treatment we recognize 5 classes, 20 orders, 34 families, 88 genera, and 174 species that occur in the benthic marine communities in Puerto Rico. Date, place, and author(s) of valid publication for all genera and species; type locality information; and descriptive accounts of vegetative morphological and reproductive anatomy are provided. Distribution of each species is given, and where relevant, comments on their habitat and taxonomic and nomenclature are discussed. A key to the genera and keys to species within genera are included. Either an in situ or other illustration accompanies most species. Three combinations: *Hydrolithon antillarum* (Foslie et M.Howe) Athanas. et D.L.Ballant. comb. nov., *Porolithon caribaeum* (Foslie) Athanas. et D.L.Ballant. comb. nov., and *Spongitis munita* (Foslie et M.Howe) Athans. et D.L.Ballant. comb. nov., are proposed. Four species, *Gracilaria cearensis* and *G. hayi*, *Corynomorpha clavata*, and *Platoma gelatinosum*, are reported as new geographic records for Puerto Rico. *Contarinia pedrochei*, *Contarinia ruizii*, *Metapeyssonnelia mesophotica*, and *Peyssonnelia tenuicrusta* are described as new species, and *Mucopeyssonnelia westii* is described as a new genus and species.

Cover images, from left to right: *Ramicrusta textilis* (Figure 134), *Ganonema vermiculare* (Figure 42), and *Peyssonnelia boergesenii* (Figure 123).

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The Marine Benthic Algal Flora of Puerto Rico, IIIA. Rhodophyta Excluding Rhodymeniales and Ceramiales

David L. Ballantine,[1]* *James N. Norris,*[1] *and Hector Ruiz*[2]

INTRODUCTION

This work is the third volume of the marine algal flora of Puerto Rico (Figure 1), covering Rhodophyta, excluding Rhodymeniales and Ceramiales. Sections on Corallinales and Sporolithales (contributed by Athanasiadis et al.) and Gracilariales (contributed by Gurgel et al.) are included in the systematic treatment. The first volume, *The Marine Benthic Algal Flora of Puerto Rico, I. Ochrophyta: Phaeophyceae, Pelagophyceae, and Xanthophyceae* (Ballantine et al. 2021), covered 77 species of Puerto Rican brown algae, including 1 new species, an account of habitat types for the island, and a history of phycology in Puerto Rico. The second volume, *The Marine Benthic Algal Flora of Puerto Rico, II. Chlorophyta and Prasinodermatophyta* (Ballantine et al. 2023), reported 150 green algal species.

Collector abbreviations used in the text are defined as follows:

AA	Athanasios Athanasiadis
DLB	David L. Ballantine
D&ML	Diane and Mark Littler
FPDB	Manuel Diaz-Pifferer
HR	Hector Ruiz
LRA	Luis Raul Almodóvar
MAH	Marshall A. Howe
MDP	Manuel Díaz-Piferrer

ATTRIBUTIONS AND METHODS

Authority names of taxa are abbreviated according to Brummitt and Powell (1992), and herbarium abbreviations follow the New York Botanical Garden's Index Herbariorum (https://sweetgum.nybg.org/ih/). Unless otherwise indicated, in situ photos, laboratory-based photographs, and herbarium specimen scans are of algae from Puerto Rico. We have followed the taxonomic arrangement of Wynne (2022). Within orders, subordinate taxa are alphabetically arranged. Type and type localities are from original publications where possible. Species distributions are mostly culled from Taylor (1960), Guiry and Guiry (2024), and original literature. Keys and species accounts are only partially original as much of the information herein has been assembled from a variety of sources. Portions of keys and taxa accounts are derived from original literature (cited with corresponding taxa) in addition to

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FIGURE 1. Map of Puerto Rico showing frequent collection sites. The depth contour surrounding the island represents a depth of 50 m. (1) Grappler Bank, (2) Caja de Muertos, (3) shelf edge off Salinas (off Guánica), (4) Punta Brea algal plain, (5) Ballena Bay, (6) Magueyes Island, (7) Media Luna algal plain, (8) Guayacan Island, (9) "Buoy," (10) Margarita Reef algal plain, (11) Punta Arenas, (12) Bajo de Sico, (13) Isabella, (14) Guajataca, (15) Islote. The scale bar in the La Parguera inset = 2.0 km.

the compilations of Taylor (1960), Abbott and Hollenberg (1976), Schneider and Searles (1991), Dawes and Mathieson (2008), Huisman (2018), and Guiry and Guiry (2024). Within distributions, we use, for convenience, "Netherlands Antilles" for records pertaining to Aruba, Bonaire, and Curaçao. As a political entity, the Netherlands Antilles was officially dissolved in 2010.

KEY TO THE RED ALGAL GENERA OF PUERTO RICO EXCLUDING RHODYMENIALES AND CERAMIALES

1. Algae forming unicellular, filamentous, pseudo- or parenchymatous aggregations lacking carpogonial branches (Bangiophycidae) 2
   Algae with pseudoparenchymatous organization and apical growth forming external carpogonia branches (1- to 4-celled) bearing distinctive trichogynes (Florideophycidae) 7
2. Algae visible to the naked eye, main branches of irregular thickness with many cells scattered within the peripheral jelly . . . . . *Bangiopsis*
   Algae not visible to the naked eye, microscopic, of filamentous construction 3
3. Thalli consisting of filaments that form microscopic disks; the filaments compact or loosely conjoined 4
   Filaments erect 5
4. Filaments closely placed to form a compact disk . . . . . *Erythrocladia*
   Filaments loosely conjoined . . . . . *Sahlingia*
5. Filaments unbranched . . . . . *Erythrotrichia*
   Filaments branched 6
6. Cells elongate, greenish gray. . . . . *Chroodactylon*
   Cells short, rose red . . . . . *Stylonema*
7. Thallus impregnated with calcium carbonate or thallus is semi-calcified 8
   Thallus lacking calcification 42
8. Calcification restricted to specialized calciferous cells. 9
   Calcification generally occurring in the walls of vegetative cells or hypobasally 10

9. Thallus cartilaginous in texture . . . . . ***Rhodogorgon***
   Thallus soft and lubricous . . . . . ***Renouxia***
10. Calcification mostly complete. 11
    Calcification weak or limited to distinct thallus parts. 12
11. Thalli with tetra/bisporangia in nemathecia 13
    Thalli with tetra/bisporangia in conceptacles 26
    Thalli with tetrasporangia in individual chambers . . . . . ***Sporolithon***
12. Calcification hypobasal, at least in part; thalli possess a "*Peyssonnelia*-like" organization in which at least part of the thallus possesses a hypothallus layer that gives rise to assurgent filaments 14
    Thalli soft, with weak development of calcification throughout the thallus, or if jointed, thalli may be compressed with finger pressure 16
13. Thalli with monostromatic hypothallus producing erect perithallial filaments; secondary pit connections are frequently formed between adjacent perithallial cells . . . . . ***Ramicrusta***
    Thalli with a mesothallus . . . . . ***Polystrata***
14. Thalli showing deviations from a "*Peyssonnelia*-like" organization in which the hypothallus periodically gives rise to upwardly (superior) and downwardly (inferior) directed filaments or where either a median-positioned perithallial cell cuts off a lateral that subsequently behaves as a hypothallus or cells of a perithallial filament cut off branches laterally and those filaments all arch dorsally and reach the dorsal surface. . . . . ***Metapeyssonnelia***
    Thalli not as above. 15
15. Assurgent filaments are laterally coherent and not immersed in mucilage. . . . . ***Agissea/Peyssonnelia***
    Assurgent filaments laterally independent and immersed in mucilage . . . . . ***Mucopeyssonnelia***
16. Calcification limited to medulla or outer portion of medulla 17
    Thalli not as above. 18
17. Thalli terete, mucilaginous; medullary filaments little calcified . . . . . ***Trichogloea***
    Thalli compressed to bladelike; thallus surface is whitish due to calcification; large granular gland cells borne by medullary filaments present . . . . . ***Titanophora***
18. Thalli not rigid, branches with obvious filamentous outer cortex (readily squashed with coverslip after decalcification), color often whitish 19
    Thalli with pseudoparenchymatous cortex, more or less rigid 24
19. Thalli not substantially calcified; thalli soft; terminal cells of assimilatory filaments are larger than subterminal cells . . . . . ***Helminthocladia***
    Thalli generally variably calcified; terminal cells of assimilatory filaments are not larger than subterminal cells. 20
20. Carpogonium dumbbell shaped . . . . . ***Helminthora***
    Carpogonium not as above 21
21. Cystocarps naked except for sterile rhizoids produced by the gonimoblast that grow downward to envelop carpogonial branch . . . . . ***Trichogloeopsis***
    Downward-growing sterile rhizoids not produced by the gonimoblast. 22
22. Medullary filaments less than 40 µm in diameter . . . . . ***Liagora/Titanophycus***
    Medullary filaments greater than 40 µm in diameter 23
23. A calcified cylinder surrounds the medulla and encompasses the inner cortical filaments; carpogonial branches are borne in median positions on assimilatory filaments . . . . . ***Gloiocallis***
    Calcification not as above; carpogonial branches are borne in a specialized branch system at the base of assimilatory filaments . . . . . ***Ganonema***
24. Algae with filamentous tetrasporophytes (heteromorphic generations). . . . . ***Tricleocarpa***
    Algae with an isomorphic alternation of generations (or nearly so) 25
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    Thalli with regular unattached superimposed growth; canals of multiporate conceptacles pyriform ..... *Magnephycus*
31. Thalli encrusting, producing erect protuberances ..... *Melyvonnea*
    Thalli encrusting, lacking erect protuberances ..... *Mesophyllum*
32. Thalli with secondary pit connections; cell fusions absent or rare 33
    Thalli with cell fusions; secondary pit connections absent or rare 35
33. Thalli erect and geniculate; hypothallus filamentous rarely detected in field collections ..... *Amphiroa*
    Thalli encrusting with monostromatic hypothallus (heterotrichous organization) 34
34. Thalli mainly epiphytic, to 3.0 cm in extent, lacking erect perithallial protuberances; hypothallus composed of sinuate cells ..... *Titanoderma*
    Thalli larger, epizoic or epilithic; erect or decumbent perithallial protuberances present in most species; hypothallus composed of palisade, trapezoid, squarish, or rhomboid cells ..... *Lithophyllum*
35. Thalli with encrusting base and erect geniculate fronds 36
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    Thalli mainly epiphytic or epizoic, of small size (to 2.0–3.0 cm); perithallus thin or lacking; trichocytes usually occurring among hypothallial cells 40
40. Trichocytes terminal on hypothallial or short perithallial filaments (around conceptacles); pore cells protruding perpendicularly in the canal of tetra/bisporangial conceptacles ..... *Fosliella*
    Trichocytes intercalary in hypothallial filaments or lacking; pore cells protruding laterally in the canal of tetra/bisporangial conceptacles ..... *Pneophyllum*
41. Spermatangia occur on the floor, walls, and roof of the chamber, and carposporangia are positioned across the dorsal side of the fusion cell ..... *Neogoniolithon*
    Spermatangia restricted to the chamber floor, and carposporangia borne from the periphery of the fusion cell; thalli encrusting lacking erect protuberances; trichocytes in horizontal series ..... *Porolithon*
    Spermatangia restricted to the chamber floor and carposporangia borne from the periphery of the fusion cell; thalli fruticose with erect protuberances; trichocytes rare or lacking ..... *Spongitis*
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    Thalli not as above 51

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Thalli not as above. 62
62. Thalli terete or flattened, radially or pinnately branched; firmly gelatinous; cortex of cells in anticlinal series . . . . . *Phyllymenia/Grateloupia* (in part)
Cortex cells not in anticlinal series. 63
63. Thalli flat or compressed . . . . . *Halymenia*
Thalli terete, dichotomously branched . . . . . *Sebdenia*
64. Thalli with a distinct central axial filament, which is surrounded by a few branched filaments; ultimate branching plumose. . . . . *Asparagopsis* (in part)
Thalli not as above. 65
65. Thallus medulla containing stellate cells. 66
Medulla not containing stellate cells. 67
66. Thalli peltate . . . . . *Meredithia*
Thalli not peltate, possessing a midrib or else having a crenulate margin, medullary filaments very densely placed. . . *Cryptonemia*
67. Thalli mostly terete, bearing numerous short, more or less acute branchlets. . . . . *Eucheumatopsis*
Thalli not as above. 68
68. Thalli creeping, segmented at intervals . . . . . *Catenella*
Thalli not as above. 69
69. Thalli biaxial (with 2 distinct apical cells). Central region of thallus with relatively few filaments; filaments of variable thickness . . . . . *Ochtodes*
Thalli not as above. 70
70. Cortex of fascicles of anticlinal rows . . . . . *Dermocorynus/Grateloupia* (in part)
Thalli not as above. 71
71. Thalli consist of blades (less than 1 cm broad) . . . . . *Flahaultia*
Thalli not as above. 72
72. Thalli are club shaped . . . . . *Corynomorpha*
Thalli not as above. 73
73. Thalli cartilaginous, margins papillose or spiny; cystocarps generally in papillae . . . . . *Meristotheca*
Thalli fleshy in consistency. 74

74. Thalli peltate or with peltate branches . . . . . *Meredithia*
Thalli not as above 75
75. Medullary filaments scattered; cystocarps 0.5–1.0 mm diam. . . . . *Solieria*
Medullary filaments intertwined; cystocarps 1.0–2.0 mm diam. . . . . *Agardhiella*
76. Thalli narrowly strap-shaped with cortical cells arranged in anticlinal rows . . . . . *Gymnogongrus*
Thalli not as above 77
77. Medulla of large cells that grade toward smaller size toward the periphery; tetrasporangia scattered 78
Thalli not as above 79
78. Thalli at most 1–2 mm in diameter in lower parts . . . . . *Gracilariopsis*
Thallus cartilaginous, decumbent or erect and compressed to flattened; branches 3.0–6.0 mm in diameter . . . . . *Crassiphycus/Gracilaria*
79. Growth from a single apical cell 80
Branch tips multiaxial 83
80. Thalli with a tough, wiry makeup; cortex and medullary cells of similar size 81
Thalli not wiry; medullary cells larger than cortical cells . . . . . *Hypnea/Calliblepharis*
81. Rhizines absent 82
Rhizines present . . . . . *Gelidium/Pterocladiella*
82. Erect axes to 2.0 mm tall or less . . . . . *Millerella*
Erect axes greater than 10 cm tall . . . . . *Gelidiella*
83. Algae more or less prostrate; cells of central medulla thin walled; sporangia zonate . . . . . *Wurdemannia*
Algae normally erect; branches palmately divided; cells of central medulla somewhat thick walled; sporangia tetrahedrally divided . . . . . *Gelidiopsis*

Rhodophyta Species Excluding Rhodymeniales and Ceramiales

Rhodophyta Wettst.

Proteorhodophytina Muñoz-Gómez, Mejía-Franco, Durnin, Colp, Grisdale, J.M.Archibald et Slamovits

Compsopogonophyceae G.W.Saunders et Hommers.

Erythropeltales Garbary, G.I.Hansen et Scagel

Erythrotrichiaceae G.M.Smith

Erythrocladia Rosenv.

Erythrocladia Rosenv. 1909: 71.

Thalli are disk-shaped arrangements of microscopic creeping filaments that radiate from the site of original spore germination. The disks are formed from filaments unified centrally but are free at their irregular margins. Disks may remain monostromatic or become polystromatic with age. Cells lack pit connections, and possess a single, parietal plastid with a central pyrenoid. Reproduction is by monosporangia that are cut off from vegetative cells. Eight *Erythrocladia* species are recognized taxonomically, one of which occurs in Puerto Rico.

Note: Guiry and Guiry (2024) caution that the genus is probably not monophyletic because of its simple conserved morphology.

Erythrocladia endophloea M.Howe

Erythrocladia endophloea M.Howe 1914: 81, pl. 30: figs. 1–7.

Heterotypic Synonyms: Erythrocladia recondita M.Howe et Hoyt 1916: 112, pl. 12: figs. 1–5, pl. 13: fig. 1; *Erythrocladia vagabunda* M.Howe et Hoyt 1916: 115, pl. 12: figs. 6–11, pl. 13: fig. 2.

Puerto Rican Records: Almodóvar and Ballantine 1983; Ballantine and Wynne 1986; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: United States, Cuba, Puerto Rico.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Bay of Sechura, Illescas Peninsula, Peru.

Thalli are endophytic or pseudo-epiphytic, consisting of microscopic, irregularly radiating filaments that inhabit the superficial cell walls of other algae. Algae are suborbicular or suborbicular-pulvinate disks that attain a diameter of 2.5 mm. They are mostly monostromatic but often irregularly form 2–4 layers in the central portion. Cells measure 3.0–15 µm diam. and 8.0–40 µm long. Branching is lateral or subdichotomous, occurring mostly in subterminal cells. Monospores originate in intercalary cells.

Habitat and Comments: Algae are endophytic within the cell wall mucilage of other, typically shallow water, algae. [Illustrations: as *Erythrocladia recondita* Howe and Hoyt 1916: pl. 12: figs. 1–5; pl. 13: fig. 1; as *Erythrocladia vagabunda*, Howe and Hoyt 1916: pl. 12: figs. 6–11; pl. 13: fig. 2.]

Erythrotrichia Aresch.

Erythrotrichia Aresch. 1850: 435, nom. cons.

Erect filaments are uni- or multiseriate and originate from small multicellular and disciform basal disks. Filament cells are subquadrate to rectangular. Vegetative cells possess a stellate plastids with a central pyrenoid. Monosporangia are segregated from vegetative cells by oblique walls. The life history involves an alternation of heteromorphic generations with the sporophytic generation being a "conchocelis" phase. One of the 31 recognized *Erythrotrichia* species is known from Puerto Rico.

Note: As with the genus *Erythrocladia*, Guiry and Guiry (2024) caution that because of its simple conserved morphology, the genus is probably not monophyletic.

Erythrotrichia carnea (Dillwyn) J.Agardh

Erythrotrichia carnea (Dillwyn) J.Agardh 1883: 15, pl. 1: figs. 8–10.
Basionym: Conferva carnea Dillwyn 1807: pl. 84.
Puerto Rican Records: As *Erythrotrichia carnea*: Díaz-Piferrer 1963; Almodóvar 1964a, 1965; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a; Ballantine et al. 2001; Ballantine and Aponte 2002a.
Western Atlantic Distribution: United States (Maine, Connecticut, New Jersey, Virginia, North Carolina, Florida), Bermuda, Bahamas, Barbados, Cuba, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, U.S. Virgin Islands, Argentina, Colombia, Uruguay, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Near Loughor (Llwchwr), Glamorgan, Wales.

Thalli are simple, solitary filaments, 0.5–2.0(–8.0) cm tall. Cells of the erect axes are 16–26 µm diam. and 16–32 µm long distally; they are 9.5–13.0 µm diam. and 15–40 µm long proximally. The filaments are typically uniseriate throughout; however, they may be multiseriate distally.

Habitat and Comments: Despite being inconspicuous due to its small size, *E. carnea* is very commonly encountered as an epiphyte on larger algae, principally in shallow water. [Illustrations: Cordeiro-Marino 1978: figs. 9–12; Littler et al. 2008: 21; Cormaci et al. 2017, FP45, figs. 1–3.]

Sahlingia Kornmann

Sahlingia Kornmann 1989: 227, figs. 1–13.

Thalli are minute crustose epiphytic or epizoic disks consisting of regularly radiating filaments closely adhering to each other. Filaments are irregularly to pseudodichotomously branched. Growth is marginal; however, intercalary growth can also occur, resulting in a raised region at the center of the disk. Apical cells at the disk margin are bifurcate. Several band or cup-shaped plastids occur per cell, lacking pyrenoids. Asexual reproduction occurs through monospore production. There are seven *Sahlingia* species recognized, of which one occurs in Puerto Rico.

Sahlingia subintegra (Rosenv.) Kornmann

FIGURE 2
Sahlingia subintegra (Rosenv.) Kornmann 1989: 227, figs. 1, 6–13.
Basionym: Erythrocladia subintegra Rosenv. 1909: 73, figs. 13, 14.
Puerto Rican Records: As *Sahlingia subintegra*: Ballantine and Aponte 1997a; Ballantine et al. 2001; Ballantine and Aponte 2002a. As *Erythrocladia subintegra*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine et al. 2001.
Western Atlantic Distribution: United States (Connecticut, Georgia, North Carolina, Florida), Belize, Bermuda, Hispaniola, Jamaica, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Uruguay, Argentina.

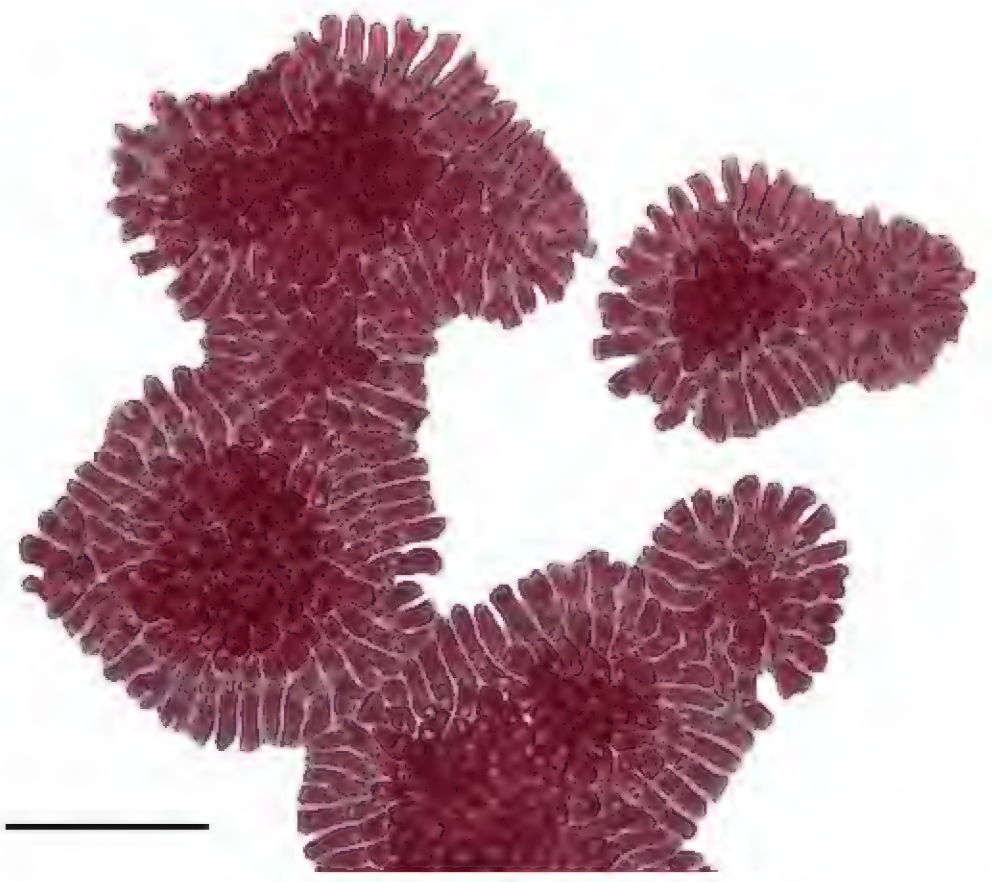

FIGURE 2. *Sahlingia subintegra*. DLBsn, Ballena Bay, Guánica, epiphytic on *Chaetomorpha* sp. Scale bar = 100 µm.

World Distribution: See Guiry and Guiry 2024.
Type Locality: Møllegrund, Skagerrak, off Hirshals, Denmark.

Thalli form small disks, to 300 µm diam. Cells are irregularly arranged and coalesce in the center and form radiating filaments, 4.0–6.0 µm diam. and 7.0–13 µm long. Cells of the radiating filaments are rectangular or irregularly shaped. Marginal cells are normally forked.

Habitat and Comments: Algae are epizoic or epiphytic on algae and seagrasses, mostly in shallow water but also dredged to 16 m depth. [Additional illustrations: as *Erythrocladia subintegra*, Børgesen 1916: figs. 3, 4; Taylor 1930: fig. 1; Schneider and Searles 1991: fig. 216; Zuccarello et al. 2010: figs. 2, 3; Cormaci et al. 2017: FP49, fig. 3.]

Stylonematophyceae H.S.Yoon, K.M.Müll., Sheath, F.D.Ott et D.Bhattacharya

Stylonematales H.S.Yoon, K.M.Müll., Sheath, F.D.Ott et D.Bhattacharya

Stylonemataceae K.M.Drew

Bangiopsis F.Schmitz

Bangiopsis F.Schmitz 1896: 314.

Thalli are gelatinous with simple filaments becoming sparingly or proliferously branched. The younger filaments are uniseriate, and older filaments become thickened by repeated irregular division. Cells possess radiating plastids. Sixteen *Bangia* species are recognized; one of these is known to Puerto Rico.

Bangiopsis subsimplex (Mont.) F.Schmitz

FIGURE 3
Bangiopsis subsimplex (Mont.) F.Schmitz 1896: 315.
Basionym: Compsopogon subsimplex Mont. 1850: 299 [Montagne 1850].
Misapplied Name: Bangiopsis humphreyi (Collins) Hamel 1929: 57.
Puerto Rican Records: As *Bangiopsis humphreyi*: Almodóvar and Blomquist 1965. As *Bangiopsis subsimplex*: Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a; Müller et al. 2001; Ballantine and Aponte 2002a; West et al. 2005.
Western Atlantic Distribution: Hispaniola, French Guiana, Martinique, Puerto Rico, Brazil.
World Distribution: See Guiry and Guiry 2024.
Type Locality: "Hab: Ad rupes maritimas aestu decedente nudatas et tum aqua dulci irrigatas prope Cayenne lectas" [French Guiana].

Bangiopsis subsimplex is the type species of the genus. Thalli comprise subsimple filaments within a gelatinous matrix. Attached by a basal disk, thalli are up to 1.5 mm in height (Almeida 2013). Filaments are irregularly pluriseriate proximally; however, they become uniseriate in the apical region. Filaments measure 35–50 µm diam. proximally and 18–24 µm diam. distally. The filaments are flexuous and sometimes proliferous. Branchlets measure 10 µm diam. Reproduction is unknown. Algae are dark purple to nearly black in color.

Habitat and Comments: All Puerto Rican records are from rocks in shallow water at the mouth of the Guajataca River. There is a question concerning which species of *Bangiopsis* is found in Puerto Rico (Almodóvar and Blomquist 1965). *Bangiopsis subsimplex* is morphologically similar to *B. dumontioides* (P.Crouan et H.Crouan) V.Krishnam., although the latter differs by having a thicker thallus and multiseriate primary ramifications (Børgesen 1915; Krishnamurthy 1957). Nevertheless, sequence analysis of specimens collected at Guajataca by T. Rintoul and A. Sherwood that were subsequently published by Müller et al. (2001) resolved the entity as *B. subsimplex*. [Additional illustrations: Børgesen 1916: fig. 5; West et al. 2005: figs. 18–23; Almeida et al. 2013: fig. 1A–J.]

FIGURE 3. *Bangiopsis subsimplex*. DLB6494, Guajataca, intertidal rocks mouth of freshwater stream. Scale bar = 500 µm.

Chroodactylon Hansg.

Chroodactylon Hansg. 1885: 14.

Thalli consist of uniseriate pseudofilaments of globose or oval cells irregularly enclosed in a gelatinous sheath. Filaments are simple or are unilaterally or pseudodichotomously branched. Each cell possesses a blue-green stellate, axial plastid, and a single pyrenoid. Cells measure 3.0–16 µm diam. and 6.0–20 µm long. Reproduction is asexual through production of monospores and fragmentation. Sexual reproduction has not been observed. One of the three recognized *Chroodactylon* species occurs in Puerto Rico.

Chroodactylon ornatum (C.Agardh) Basson

Chroodactylon ornatum (C.Agardh) Basson 1979: 67, pl. IX: fig. 52.

Basionym: Conferva ornata C.Agardh 1824: 104.

Heterotypic Synonym: *Asterocytis ramosa* (Thwaites) Gobi ex F.Schmitz 1896: 314.

Puerto Rican Records: As *Asterocytis ramosa*: Díaz-Piferrer 1963; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a. As *Chroodactylon ornatum*: Ballantine et al. 2001; Ballantine and Aponte 2002a.

Western Atlantic Distribution: United States (Massachusetts, Connecticut, Virginia, North Carolina, Florida), Bahamas, Grenada, Hispaniola, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela, Argentina.

World Distribution: See Guiry and Guiry 2024.

Type Locality: "In lacu Malaren ad pontem prope Traneberg" [bridge near Transberg, Lake Mälaren, near Stockholm, Sweden (Brodie and Irvine 2003)].

Thalli are simple uniseriate filaments that measure 1.0–10 mm high and 12–20(–25) µm diam. Branching is unilateral or subdichotomous. Cells of the filaments are oval to elongate, measuring 5.0–8.0 µm diam. and 8.0–20 µm long. Algae are pale steel green in color.

Habitat and Comments: *Chroodactylon ornatum* grows as epiphytes on algae and seagrasses and is inconspicuous, requiring microscopic examination of the host for recognition. Taylor (1960, as *Asterocytis ramosa*) reported that *C. ornatum* occurs in tufts; however, Puerto Rican specimens are generally found growing solitarily. [Illustrations: as *Asterocytis ramosa*, Børgesen 1916: fig. 1; as *Chroodactylon ornatum*, Cormaci et al. 2017: FP55, fig. 1.]

Stylonema

Stylonema Reinsch 1875: 40.

Minute thalli, embedded in a mucilaginous matrix, consist of pseudodichotomously branched or unbranched pseudofilaments that are uniseriate or pluriseriate. Filament cells possess a single stellate plastid containing a large central pyrenoid. Thalli are attached by an unmodified or slightly enlarged basal cell. Asexual reproduction occurs through transformation of a vegetative cell to an archeospore that is released from the gelatinous matrix. Sexual reproduction is unknown. Nineteen species of *Stylonema* are recognized worldwide; only one of these occurs in Puerto Rico.

Stylonema alsidii (Zanardini) K.M.Drew

Stylonema alsidii (Zanardini) K.M.Drew 1956: 72.

Basionym: *Bangia alsidii* Zanardini 1840: 136.

Homotypic Synonym: Goniotrichum alsidii (Zanardini) M.Howe 1914: 75.

Puerto Rican Records: As *Goniotrichum alsidii*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983. As *Stylonema alsidii*: Hinds and Ballantine 1987; Ballantine and Aponte 1997a; Ballantine et al. 2001; Ballantine and Aponte 2002a.

Western Atlantic Distribution: Belize, United States (New Hampshire, Massachusetts, Connecticut, New Jersey, Virginia, North Carolina, Georgia, Texas, Florida), Bermuda, Bahamas, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, Trinidad and Tobago, Barbados, U.S. Virgin Islands, Brazil, Brazil, Venezuela, Uruguay, Argentina.

World Distribution: See Guiry and Guiry 2024.

Type Locality: "Ad *Alsidium* Ag. sub microscopic species pulcherrima." Trieste, Italy.

Thalli typically consist of irregularly to pseudodichotomously branched uniseriate or pluriseriate pseudo-filaments within a gelatinous matrix. The filaments measure 0.3–6.0 mm high and 12–20 µm diam. and are thickened at the base to 30–50 µm diam. Thalli occur solitarily or in tufts. Cells are discoid to ellipsoid or nearly cylindrical, 7.0–13 µm diam. and 4.0–13 µm long.

Habitat and Comments: The species is typically collected as epiphytes on other algae and seagrasses. As is the case for the previous species, *Stylonema alsidii* is microscopic and will be observed only during microscopic examination of the basiphyte. [Illustrations: as *Goniotrichum elegans*, Børgesen 1916: fig. 2; Feldmann 1939: fig. 3; Schneider and Searles 1991: fig. 211; Littler et al. 2008: 20; Won et al. 2010: figs. 13, 14; Cormaci et al. 2017: FP55, figs. 4, 5.]

Florideophyceae Cronquist

Ahnfeltiophycidae G.W.Saunders et Hommers.

Pihiellales Huisman, A.R.Sherwood et I.A.Abbott

Pihiellaceae Huisman, A.R.Sherwood et I.A.Abbott

Pihiella Huisman, A.R.Sherwood et I.A.Abbott

Pihiella Huisman, A.R.Sherwood et I.A.Abbott, 2003: 981.

Thalli are minute endophytic or epiphytic pseudoparenchymatous discoid to subspherical structures, attached by rhizoids. Reproduction occurs in sporangia, with spores measuring

20–25 µm long and 15–20 µm diam. Spermatangia mother cells are borne on the surface. Members of the monotypic genus are associated with and grow within Liagoraceae species.

Pihiella liagoraciphila Huisman, A.R.Sherwood et I.A.Abbott

Pihiella liagoraciphila Huisman, A.R.Sherwood et I.A.Abbott 2003: 981, figs. 1–4.
Puerto Rican Records: Ballantine et al. 2004.
Western Atlantic Distribution: Jamaica, Puerto Rico.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Mokulëʻia, Oahu, Hawaiian Islands.

Pihiella liagoraciphila is the type species of the genus. Thalli are attached by rhizoids and filaments. The discoid algae are endophytic to epiphytic, measuring to 400 µm diam. and to 150 µm in thickness. Spore dimensions are those given in the genus account.

Habitat and Comments: Puerto Rican algae are endophytic within *Liagora* thalli and measure 40 to 150 µm in diameter. Prior to the Huisman et al. (2003) formal description of the genus and species, these enigmatic algae from the Caribbean were considered to be "monosporangial discs" by Howe (1920a). The species is highly inconspicuous, and its distribution is undoubtedly much greater than is indicated by the literature, probably occurring throughout the Caribbean region. [Illustrations: Howe 1920a: figs. 1–15; Huisman 2018: fig. 189.]

Corallinophycidae L.Le Gall et G.W.Saunders[1]

Corallinales P.C.Silva et H.W.Johans.

Corallinaceae J.V.Lamour.

Corallinoideae S.F.Gray

Corallineae Naccari

Corallina L.

Corallina L. 1758: 646, 805.

Thalli possess crustose discoid holdfasts and bear one to several erect, pinnately branched, geniculate axes. The erect axes comprise wedge-shaped calcified segments (intergenicula) separated by uncalcified genicula. Intergenicula are terete to compressed and pinnately branched, frequently complanate. They consist of 8–25 tiers of medullary cells surrounded by a photosynthetic cortex and a unistratose layer of epithallial cells. Cells in adjacent filaments often fuse, and secondary pit connections do not form. Genicula consist of single tiers of elongated unbranched cells. Conceptacles are uniporate and occur terminally or laterally on intergenicula. Gametophytes are dioecious. Carpogonial conceptacles develop a layer of supporting cells, each supporting a 2-celled carpogonial filament. Carposporangia develop from the periphery and somewhat inward from the upper edge of a conspicuous fusion cell. Conceptacles sometimes bear lateral branches. One of the 28 recognized *Corallina* species occurs in Puerto Rico.

Corallina panizzoi Schnetter et U.Richt.

FIGURE 4
Corallina panizzoi Schnetter et U.Richt. 1979: 462, figs. 1, 2B, 3–5, pl. 2.
Heterotypic Synonym: *Corallina officinalis* var. *fastigiata* Kütz. 1849: 705.
Misapplied Name: Corallina officinalis L. 1758: 805.
Puerto Rican Records: As *Corallina officinalis*: Navarro and Almodóvar 1974; Almodóvar et al. 1979. As *Corallina panizzoi*: Schnetter and Richter 1979; Ballantine and Aponte 1997a, 2002a.
Western Atlantic Distribution: Puerto Rico, Venezuela, Colombia.
Type Locality: Puerto Cabello, Venezuela.

Epilithic thalli, 3.0–8.0 cm tall, arise from a basal disk and produce several erect axes that are subdichotomously or trichotomously divided. Proximal intergenicula measure 0.4–1.0 mm broad and 0.4–2 mm long, whereas at mid thallus, they are 0.7–1.5 mm broad and 1.4–4.5 mm long. Distal segments are subdi- to tetrachotomously branching, measuring 0.3–0.9 mm broad and up to 7.2–9.0 mm long. Segments in the upper thallus are slightly compressed and cuneate. Intergenicular medullary cells are 30.5 to 50.5 µm long and 3.3 to 5.5 µm broad, and genicular medullary cells are 137–383 µm long and 6–10 µm broad. Conceptacles of tetrasporophytes and carposporophytes are hemispherical, whereas male conceptacles are conical.

Habitat and Comments: *Corallina panizzoi* is probably widespread in the Caribbean, often occurring in dense growths. It is typically found intertidally and in shallow water, sometimes growing in water of moderate depth. Our account is based on the protologue of Schnetter and Richter (1979: 460–466), in which the species is distinguished from *C. officinalis* in having shorter intergenicular medullary cells. In particular, in *C. panizzoi* these are 30.5–50.5 µm long, whereas in *C. officinalis* they are 58.4 to 88.1 µm long (50–90 µm in British specimens according to Irvine and Johansen 1994: 45). Schneider and Searles (1991: 228) reported a size of 36–60 µm in records of *C. officinalis* from North Carolina, measurements that more or less correspond to the size found in *C. panizzoi*. Nevertheless, North and South Carolina records of a cosmopolitan *C. officinalis* have been included under the molecular concept of *Corallina berteroi* Kütz. (Calderon et al. 2021: figs. 2–4). Yet the original material of *C. berteroi* differs in producing up to 6 branches from a segment and in having a compact thallus with shorter segments that are distinctively expanded laterally throughout their length. In some cases, a midrib is discernable (Kützing 1858: pl. 65: fig. IIc–e). Both species are included in Wynne's (2022) checklist of benthic marine algae of the tropical and subtropical Western Atlantic.

[1] Contributed by A. Athanasiadis (Herbarium GB, Göteborgs, Universitet, Inst. för Biologi och Miljövetenskap. Box 463, 405 30 Göteborg, Sweden), D. L. Ballantine, J. N. Norris, and H. Ruiz.

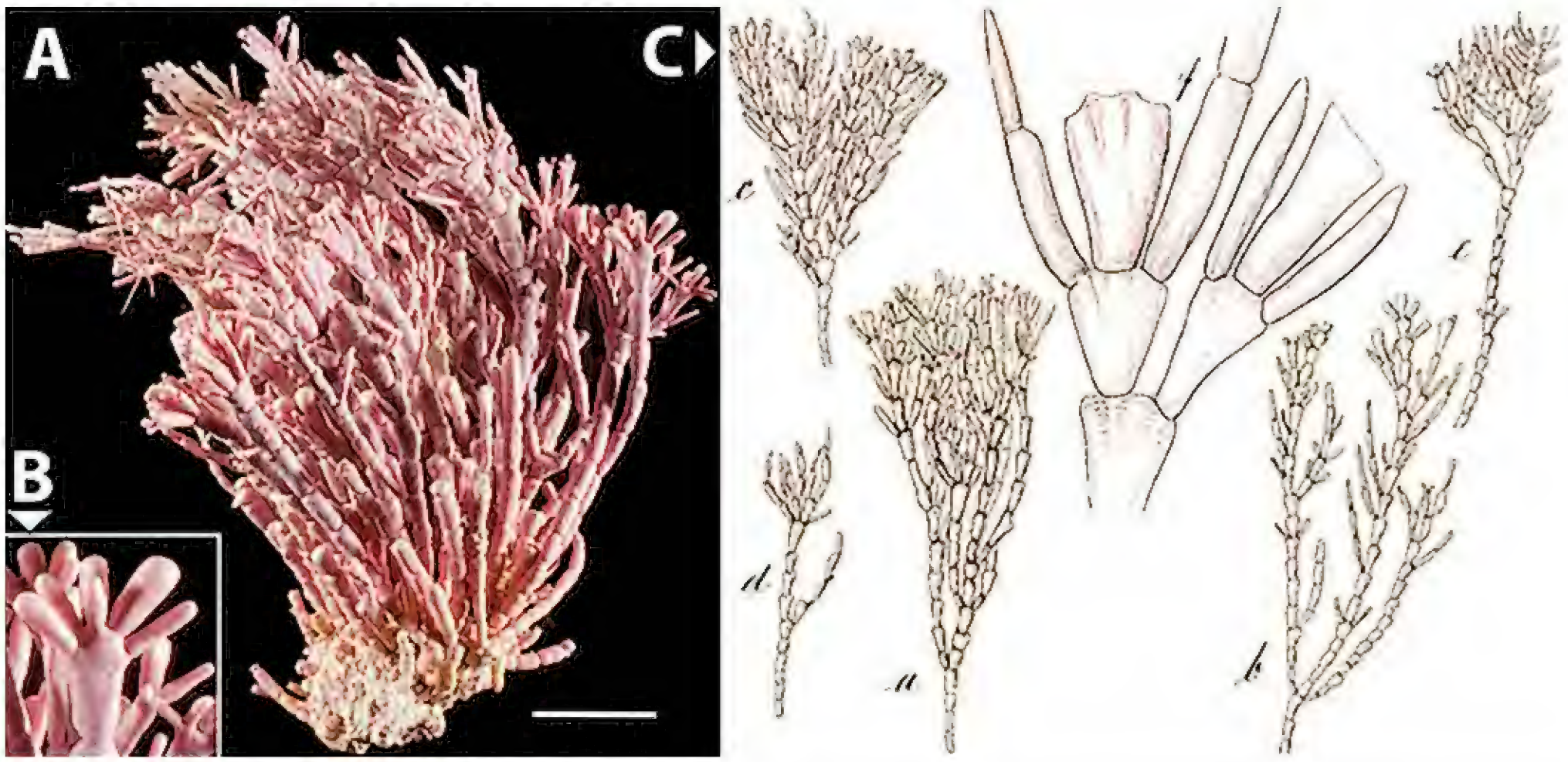

FIGURE 4. *Corallina panizzoi*. (A) Live specimen, Guajataca intertidal. Scale bar = 1.0 cm. (B) Apical segments. (C) Type specimens from Puerto Cabello (Kützing 1858: pl. 67: fig. Ia–f, no scale).

[Additional illustrations: as *Corallina panizzoi*, Schnetter and Richter 1979: figs. 1, 2B, 3–5; as *Corallina officinalis* var. *fastigiata*, Kütz. 1858: pl. 67: fig. Ia–f.]

Janieae H.W.Johans. et P.C.Silva

Haliptilon (Decne.) Lindley

Haliptilon (Decne.) Lindley 1846: 25.

Thalli are heavily calcified and consist of a crustose base producing erect geniculate fronds to 5.0 cm tall. Primary branching is subdichotomous, and secondary branching is pinnate. Adventitious branches are present. Thalli mostly occur on hard substrata or as epiphytes. Intergenicula are terete to compressed and cuneate, with 3–6 tiers of medullary cells of equal length with a cortex and 1 layer of epithallial cells. Genicula comprise a single tier of elongate cells. Trichocytes and cell fusions between medullary cells are present; secondary pit connections are absent. Gametophytes are monoecious, and conceptacles are axial and terminal.

Members of *Haliptilon* were resolved in a monophyletic group by Kim et al. (2007: fig. 3) including *Jania corniculata* (L.) J.V.Lamour. that exhibits pinnate ramification and should be considered a case of parallelism. Approximately four species of *Haliptilon* are recognized worldwide, two of which occur in Puerto Rico.

KEY TO THE *HALIPTILON* SPECIES OF PUERTO RICO

1. Branching irregular and loosely pinnate; segments (intergenicula) of the main axes mostly terete . . . . . ***H. cubense***
   Branching regularly pinnate; segments of the main axes mostly flattened . . . . . ***H. subulatum***

Haliptilon cubense (Mont. ex Kütz.) Garbary et H.W.Johans.

FIGURE 5

Haliptilon cubense (Mont. ex Kütz.) Garbary et H.W.Johans. 1982: 218.

Basionym: *Jania cubensis* Mont. ex Kütz. 1849: 709–710.

Homotypic Synonym: Corallina cubensis (Mont. ex Kütz.) Kütz. 1858: 37, pl. 77: fig. 2.

Puerto Rican Records: Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002a. As *Corallina cubensis*: Díaz-Piferrer 1963; Almodóvar 1964a, 1964b, 1965; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983. As *Jania cubensis*: Ballantine et al. 2016b.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida, North Carolina), Bermuda, Bahamas, Cuba, Grenada, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto

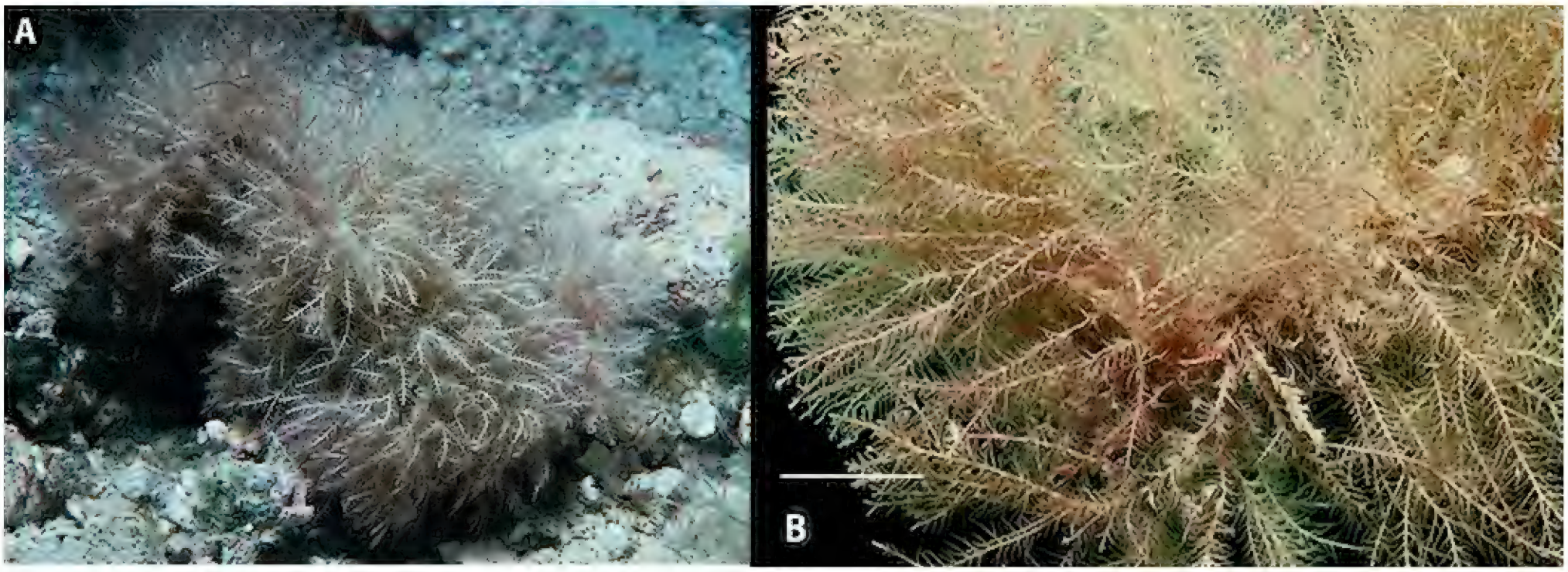

FIGURE 5. *Haliptilon cubense*. (A) In situ photograph, algal plain, seaward of Media Luna Reef, La Parguera, 17 m. Field is approximately 20 cm. (B) Detail of live specimen, Enrique Reef, La Parguera, 2.0 m. Scale bar = 1.0 cm.

Rico, Trinidad, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Cuba.

Thalli occur in dense tufts measuring to 3.0 cm tall. They are attached by a crustose calcified base as well as secondarily by calcified pads borne on branchlets. The main axes are typically oppositely branched from the distal ends of the heavily calcified segments. Branching may also be irregular, dichotomous, or pinnate. Proximal axial segments measure 100–400(–700) µm broad and 150–600 µm long. Segment dimensions decrease distally, and branchlets are to 100 µm diam. Segments consist of tiers of medullary cells, 35–100 µm long and 12 µm diam. The cortex is composed of round cells, 5.0–8.0 µm diam. Genicula comprise single tiers of elongate cells, 80–210 µm long, without a cortex. Urn-shaped tetrasporangial conceptacles possess a single apical pore and occur between hornlike projections. Zonately divided tetrasporangia measure 20–70 µm diam. and 80–120 µm long. Algae are pinkish to rose in color.

Habitat and Comments: *Haliptilon cubense* is common in Puerto Rico and is typically encountered in the intertidal as well as shallow to moderate depths. [Additional illustrations: Schneider and Searles 1991: figs. 263–265; as *Corallina cubensis*, Taylor 1960: pl. 50: figs. 3, 4.]

Haliptilon subulatum (J.Ellis et Sol.) H.W.Johans.

FIGURE 6

Haliptilon subulatum (J.Ellis et Sol.) H.W.Johans. 1970: 79, 83–84: figs. 10, 12.

Basionym: *Corallina subulata* J.Ellis et Sol. 1786: 119–120, pl. 21b,B.

Homotypic Synonym: Jania subulata (J. Ellis et Sol.) Sond. 1848: 186.

Puerto Rican Records: Ballantine and Aponte 2002a. As *Corallina subulata*: Hauck 1888; Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1964a, 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a; Ballantine et al. 2016b.

Western Atlantic Distribution: Bermuda, Bahamas, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Eustatius, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Argentina, Brazil, Colombia, Venezuela.

World Distribution: Indian Ocean (Silva et al. 1996), Mediterranean (Athanasiadis 2016).

FIGURE 6. *Haliptilon subulatum*. DLB7024, Ballena Bay, 0.5 m. Scale bar = 1.0 mm.

Type Locality: West Indies.

Thalli are erect and bushy, measuring 2.0–4.0(–5.0) cm tall, attached by a conical disk and secondarily by attachment disks from branch tips. Complanate branching is dichotomous and secondarily pinnate. Proximal segments (intergenicula) are terete to flattened, measuring 100–240 µm diam. In the central thallus portions, they are compressed, measuring 0.7–1.0 mm diam. and 0.3–0.7 mm long. Distal segments are cylindrical to flat, measuring to 60 µm diam. Flattened axial segments may be broadly deltoid and costate. Segments are composed of tiers of medullary cells, to 12 µm diam. and to 100 µm long, surrounded by a cortex of rounded cells, 5.0–7.5 µm diam. Genicular medullary cells are arranged in a single tier. Conceptacles occur on swollen tips and are situated between hornlike branchlets. Algae are rose red in color.

Habitat and Comments: *Haliptilon subulatum* frequently grows as an epiphyte on other algae in shallow water, occurring from the intertidal down to 3.0 m depths. The species is not commonly collected in Puerto Rico. [Additional illustrations: as *Corallina subulata*, Braune and Guiry 2011: fig. 130.2; Abbott 1999: figs. 46C,D, 47B,C; Littler and Littler 2000: 27; Dawes and Mathieson 2008: 193, pl. 25: fig. 13.]

Jania J.V.Lamour.

Jania J.V.Lamour. 1812: 186.

Thalli are lightly to heavily calcified and consist of a crustose base with erect, geniculate fronds, 0.1 to 10 cm tall. Some species possess decumbent branches (stolons). Thalli mostly occur on hard substrata or are epiphytes. The erect or decumbent geniculate axes are subdichotomously branched. Adventitious branches rarely occur. Intergenicula are terete to compressed or flattened and consist of elongate medullary cells, in 1–25 tiers, and a thin cortical region of 1–3 cells surrounding the medulla and terminating in a single layer of epithallial cells. Genicula consist of a single tier of unbranched medullary cells. Trichocytes occur in some species. Gametophytes can be either monoecious or dioecious. Uniporate gametangial or tetrasporangial conceptacles occur at distal ends of intergenicula and may bear lateral branches that produce further conceptacles. There are 49 species of the genus worldwide, of which 6 are known to Puerto Rico, including the generitype *J. rubens*.

KEY TO THE *JANIA* SPECIES OF PUERTO RICO

1. Thalli epiphytic in minute to 3 mm tall tufts ..... *J. pumila*
   Thalli larger 2
2. Branching angles narrow; branch tips acute ..... *J. rubens*
   Branching wide angled 3
3. Segments less than 100 µm diam. ..... *J. capillacea*
   Segments greater than 100 µm diam. ..... *J. adhaerens*

Jania adhaerens J.V.Lamour.

FIGURE 7

Jania adhaerens J.V.Lamour. 1816: 270.

Homotypic Synonym: *Jania pedunculata* J.V.Lamour. var. *adhaerens* (J.V.Lamour.) A.S.Harv., Woelk. et Reviers 2020: 247, fig. 17A–D.

Puerto Rican Records: Taylor 1960; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002a; Ballantine et al. 2016b; Sherman et al. 2023.

Western Atlantic Distribution: Belize, Caribbean Mexico, United States (Florida, North Carolina, Texas), Bermuda, Bahamas, Barbados, Cuba, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Bartholomew, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Mediterranean? Lamouroux (1816) lists the type locality with a query. Lectotype specimen selected by A. B Cribb (see Johansen 1981: 247).

Erect thalli, 1.0–4.0 cm tall, are attached primarily by a basal crust and secondarily by calcified pads borne on decumbent branches. The subdichotomous branching is wide angled (45°–60° or greater). Segments are terete,100–200 µm diam. proximally and

FIGURE 7. *Jania adhaerens*. In situ photograph, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Field is approximately 10 cm.

2–4(–6) diameters long, with conical to acute apices. Conceptacles are urn shaped, 240–300 µm across and 300–340 µm high. They are bordered by two hornlike branchlets. Zonately divided tetrasporangia measure 60–70 µm diam. and 80–100 µm long.

Habitat and Comments: *Jania adhaerens* is broadly distributed, usually occurring in shallow-water environments (Taylor 1960) on hard substratum and as epiphytes, although collections to 35 m depths have been reported (Hanisak and Blair 1988; Ballantine et al. 2016b). Harvey et al. (2020) separated *J. adhaerens* from *J. pedunculata* by the absence of swollen intergenicula in the former species, which they recognized as a variety of the latter.

However, the cosmopolitan distribution of *J. adhaerens* contrasts the restricted (Australian) occurrence of *J. pedunculata*, suggesting that their relationship should be the reverse. We therefore recognize *J. adhaerens* as a distinct species, pending further studies to clarify its cosmopolitan distribution and its relationship to *J. pedunculata*. [Additional illustrations: Schneider and Searles 1991: 266, 267; Littler et al. 2008: 29; Cormaci et al. 2017: FP199, figs. 1–2.]

Jania capillacea Harv.

FIGURE 8

Jania capillacea Harv. 1853: 84.

Puerto Rican Records: Díaz-Piferrer 1963; Almodóvar and Blomquist 1959; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Belize, Panama, Caribbean Mexico, United States (Florida, North Carolina, Texas), Bermuda, Bahamas, Barbados, Costa Rica, Cuba, Netherlands Antilles, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil, Colombia.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Bahia Honda Key, Florida, USA.

Thalli are delicate and erect, 4.0–10 mm tall, arising from basal crusts and also attached via adventitious pads produced from decumbent branches. Branch dichotomies possess wide angles (60°–90°). The segments are terete, measuring (30–)45–100(–150) µm diam. and 4–6(–10) diameters long proximally. Branch segments decrease in size distally, with apices blunt, tapered, or acute. Ultimate branchlets are sometimes recurved. Segment medullary cells are in parallel tiers, measuring 25–40 µm long, and cortical cells are 5.0–8.0 µm diam. Genicular medullary cells are 40–75 µm long and occur in a single tier. Conceptacles are compressed swellings at or near the ends of distal segments. They bear distinct hornlike projections and possess a distinct apical pore. Zonately divided tetrasporangia measure 30–40 µm diam. and 80–105 µm long. Algae are pinkish to red in color.

Habitat and Comments: *Jania capillacea* is frequently found as an epiphyte, typically in shallow-water environments as well as to moderate depths. Cribb (1983) referred *Jania capillacea* to *J. adhaerens*; however, Silva et al. (1996) maintained them as separate species. [Additional illustrations: Schneider and Searles 1991: figs. 268–169; Littler et al. 2008: 33.]

FIGURE 8. *Jania capillacea*. DLB6247, live specimen, algal plain, Punta Brea, Guánica, 17 m. Scale bar = 0.5 mm.

Jania pumila J.V.Lamour.

FIGURE 9

Jania pumila J.V.Lamour. 1816: 269, pl. 9: fig. 2.

Homotypic Synonym: Corallina pumila (J.V Lamour.) Kütz. 1858: 39.

Puerto Rican Records: Taylor 1960; Ballantine and Aponte 1997a, 2002a. As *Corallina pumila*: Hauck 1888.

Western Atlantic Distribution: Belize, Caribbean Mexico, United States (Florida), Bermuda, Cuba, Hispaniola, Jamaica, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Syntype Localities: "Mer Rouge" [Red Sea] and "Indes Orientales" [East Indies] (Lamouroux 1816).

Colony-forming thalli are generally decumbent, 0.5–1.0 cm diam. and reaching 2.0–3.0 mm in height. Axes arise from a common basal disk and are 2–3 times subdichotomously branched. Subcylindrical segments measure 60–150 µm diam. and to 200 µm long. Segment medullary cells measure 20–30 µm long and occur in parallel tiers. The rounded cortical cells are 5.0–8.0 µm diam. Genicular medullary cells measure 4.0–8.0 µm diam., occurring in 1 tier. Segments bearing conceptacles are typically triangular in shape. Spermatangial

FIGURE 9. *Jania pumila*. DLB392, herbarium specimen, offshore from Islote, Arecibo, 11 m. Epiphytic on *Stypopodium zonale* (J.V.Lamour.) Papenfuss. Scale bar = 2.0 mm.

conceptacles are typically spindle shaped. Tetrasporangial and female conceptacles are swollen and measure 250 µm diam. The conceptacles are situated between two horns that comprise 2–4 segmented branchlets.

Habitat and Comments: *Jania pumila* occurs as small epiphytes in shallow water. It has rarely been found in Puerto Rico, probably due to its inconspicuousness. It may be an exclusive epiphyte occurring only on species of Phaeophyceae. South and Skelton (2003) proposed that *Jania pumila* was synonymous with *J. tenella* (Kütz.) Grunow from Atlantic Caribbean Mexico; however, that proposal has not been followed in subsequent floral treatments (i.e., Skelton and South 2007; Dawes and Mathieson 2008; Wynne 2017, 2022). [Additional illustration: Littler and Littler 2000: 33.]

Jania rubens (L.) J.V.Lamour.

Jania rubens (L.) J.V.Lamour. 1816: 272.

Basionym: *Corallina rubens* L. 1758: 806.

Puerto Rican Records: Taylor 1960; Almodóvar 1965; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a. As *Corallina rubens*: Hauck 1888.

Western Atlantic Distribution: Belize, Caribbean Mexico, United States (Florida, North Carolina, Texas), Bermuda, Bahamas, Cuba, Hispaniola, Honduras, Jamaica, Martinique, Puerto Rico, St. Bartholomew, St. Eustatius, Trinidad and Tobago, Turks and Caicos, Argentina, Brazil, Colombia, Uruguay, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Europe.

Thalli are tufted, frequently occurring in cushion-like growths and reaching 2.0–3.0(–8.0) cm in height. Branching is subdichotomous, with narrowly branching sinuses (10°–20°). Several segments occur between branching points. Proximal segments are terete or somewhat cask shaped and are about 2 diameters long. Segments of the central thallus portion are terete, measuring 125–200(–280) µm diam. and are 3–6(–9) diameters long. Distal segments, sometimes club shaped, decrease in diameter to 65–100 µm and possess acute apices. Segment medullary cells are tiered and measure 80–150 µm long. Segment cortical cells are rounded, measuring 7.0–13 µm diam. The single-tiered uncalcified genicula are 80–170 µm diam. Gametophytes are monoecious. Carposporangial and spermatangial conceptacles are situated in a terminal position. The former are horned, whereas the latter are fusiform in shape. Tetrasporangial conceptacles are urn shaped, with a protruding ostiole, and measure 250–300 µm long. They are situated between two hornlike branchlets of 2–3 cells. The zonately divided tetrasporangia measure 40–60 µm diam. and 100–150 µm long. Algae are pink to rose red in color.

Habitat and Comments: *Jania rubens* grows in reef environments, often on dead coral heads, and has been collected to 30 m depths. [Illustrations: Littler and Littler 2000: 32; Braune and Guiry 2011: fig. 131.1; Cormaci et al. 2017: FP203, figs. 1–3.]

LITHOPHYLLACEAE ATHANAS.

LITHOPHYLOIDEAE SETCH.

AMPHIROEAE J.CABIOCH

Amphiroa J.V.Lamour.

Amphiroa J.V.Lamour. 1812: 186.

Heavily calcified geniculate thalli are either erect or decumbent and branched subdichotomously, trichotomously, or irregularly. The hypothallus is filamentous and inconspicuous, producing the erect axes (perithallus) that are made up of terete to compressed or flattened segments (intergenicula) that are separated by uncalcified genicula (Cabioch 1988: 501, fig. 6 B). Anatomically, intergenicula possess a medulla with filaments comprising short ovoid cells that alternate with longer ones. Cortical cells are derived from medullary cells that curve outwardly and terminate in epithallial cells. Trichocytes occur among epithallial cells. Cells of adjacent filaments possess secondary pit connections; cell fusions are absent. The genicular medulla possesses 1–3 tiers of elongate cells. Gametophytes are dioecious, and gametangia and tetra/bisporangia occur in uniporate conceptacles. This is a widespread tropical and subtropical genus with some 55 recognized species, 4 of which, including the generitype *A. tribulus*, occur in Puerto Rico.

KEY TO THE *AMPHIROA* SPECIES OF PUERTO RICO

1. Segments mostly broadly flattened; branching irregular 2
   Segments terete or compressed; branching regularly dichotomous 3
2. Segments commonly with a distinct midrib . . . . . *A. tribulus*
   Segments without a midrib. . . . . *A. hancockii*
3. Segments 150–600 µm diam. . . . . *A. fragilissima*
   Segments 1.0–2.0 mm diam. . . . . *A. rigida*

Amphiroa fragilissima (L.) J.V.Lamour.

FIGURE 10

Amphiroa fragilissima (L.) J.V.Lamour. 1816: 298.

Basionym: *Corallina fragilissima* L. 1758: 806.

Puerto Rican Records: Hauck 1888; Almodóvar and Blomquist 1959; Almodóvar 1962, 1964a, 1964b, 1965; Almodóvar and Pagán 1971; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida, North Carolina, Texas), Bermuda, Bahamas, Barbados, Belize, Costa Rica, Cuba, Dominica, Grenadines, Grenada, Guadeloupe, Hispaniola, Honduras, Jamaica, Martinique, Netherlands Antilles, Panama, Puerto Rico, St. Bartholomew, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Habitat "in Indiis" [Jamaica?] (Linnaeus 1758).

Thalli are erect, to 4.0 cm tall, composed of narrow cylindrical axes that are branched subdichotomously, sometimes trichotomously, with branches diverging at roughly 45°. Segments are brittle and terete, measuring 150–600 µm diam. and are 8–20 diameters long. Characteristically, the segments are prominently swollen at their ends. Segment medullary filaments comprise 4–8 arched tiers of long cells that alternate with 1 or 2 shorter cells. The cortex is composed of cells shorter than the medullary cells. Uniporate conceptacles are formed laterally on segments, a few per segment, measuring 300–400 µm diam. Tetrasporangia measure 20–25 µm diam. and 50 µm long. Algae are yellowish to pink in color.

Habitat and Comments: Although usually solitary, *Amphiroa fragilissima* thalli can form extensive entangled mats or occur as extensive growths. The species may be collected in a variety of shallow-water environments. [Additional illustrations: Taylor 1960: pl. 47: figs. 1, 2; Littler and Littler 2000: 23; Braune and Guiry 2011: fig. 125.1; Harvey et al. 2013: figs. 25–29; Cormaci et al. 2017: FP223, figs. 1, 2.]

Amphiroa hancockii W.R.Taylor

FIGURE 11

Amphiroa hancockii W.R.Taylor 1942: 95, pl. 13: figs. 1, 2.

Puerto Rican Distribution: Díaz-Piferrer 1970; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, Panama, Hispaniola, Honduras, Martinique, Puerto Rico, St. Lucia, Colombia.

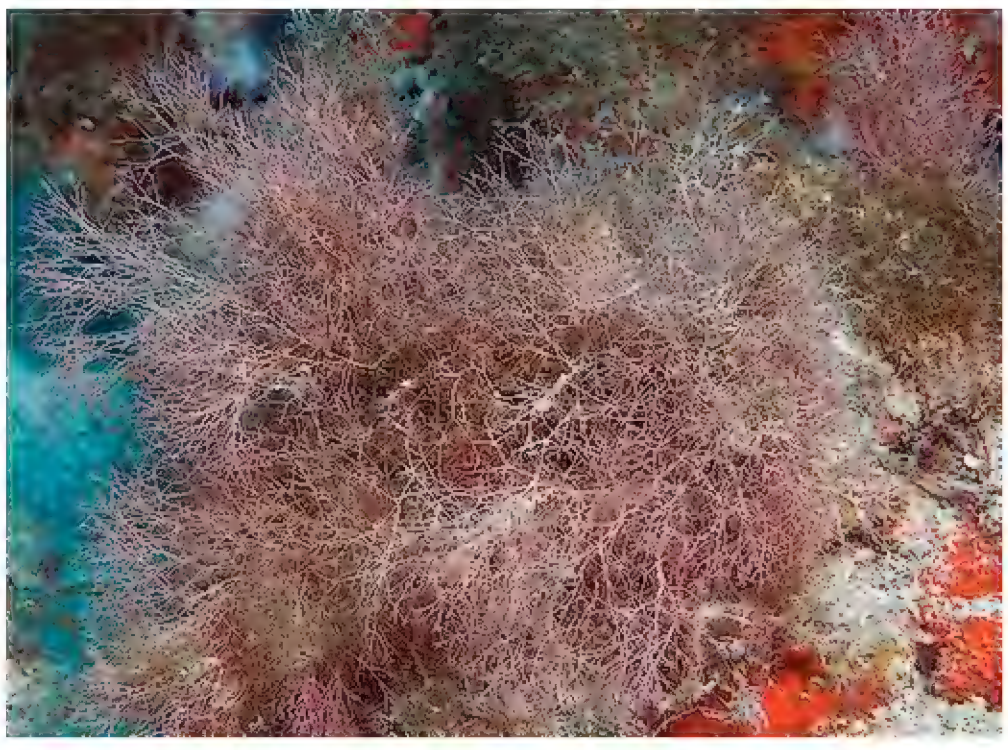

FIGURE 10. *Amphiroa fragilissima*. In situ habit photograph, edge of insular shelf, offshore from La Parguera, 18 m. Field width = approximately 15 cm.

FIGURE 11. *Amphiroa hancockii*. In situ habit photograph, edge of insular shelf, offshore from La Parguera, 18 m. Field width = approximately 8.0 cm.

World Distribution: See Guiry and Guiry 2024.
Type Locality: Bahia de Caledonia Harbor, Panama.

Heavily calcified thalli reach to 8.0 cm tall. Branching is irregular to tri-tetrachotomous, with numerous adventitious branches. Segments, 3.0–8.0 mm diam. and to 30(–60) mm long, are subterete to compressed. Adventitious branches are flat or triangular, and segments themselves are sometimes branched. Segment medullary cells consist of tiers of 1 or 2 long cells, to 100 µm long, alternating with a tier of shorter cells, 8.0–30 µm long. The multilayered cortex consists of short cells. Conceptacles are little elevated, measuring 210–270 µm diam., and possess a single inconspicuous pore. Tetrasporangia measure 15–20 µm diam. and 30–50 µm long. Algae are pinkish purple in color.

Habitat and Comments: *Amphiroa hancockii* is typically found in coral reef environments. [Additional illustration: Littler and Littler 2000: 23.]

Amphiroa rigida J.V.Lamour.

FIGURE 12

Amphiroa rigida J.V.Lamour. 1816: 297, pl. 11: fig. 1.

Heterotypic Synonym: Amphiroa rigida var. *antillana* Børgesen 1917: 182, figs. 171–173.

Puerto Rican Records: As *Amphiroa rigida* var. *antillana*: Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1962, 1964a; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a; Ballantine et al. 2016b; Sherman et al. 2023.

Western Atlantic Distribution: Caribbean Mexico, United States (Texas), Bermuda, Bahamas, Barbados, Cuba, Guadeloupe, Hispaniola, Honduras, Jamaica, Martinique, Panama, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2024.
Type Locality: Mediterranean Sea.

Heavily calcified, brittle thalli form clumps that reach to 15 cm diam. Thalli branch subdichotomously and possess adventitious branches. The cylindrical segments themselves become unequally forked distally at dichotomies and measure 1.0–2.0 mm diam. The segments are somewhat variable in length, measuring from 1.0 to 2.0 mm long. Branch apices are obtuse. The segment medullary core comprises filaments with 2 rows of long cells, 80–100 µm long, that alternate with a single tier of short medullary cells ~20 µm long. The surrounding cortex is composed of several layers of small cells. The genicula are composed of 2 rows of elongate cells. Uniporate conceptacles are hemispherical, measuring 250–400 µm diam., and occur laterally on segments. Algae are light gray or purple in color.

Habitat and Comments: *Amphiroa rigida* is typically an alga of shallow water in a variety of habitats and has been reported down to 11 m depth (Taylor 1960). [Additional illustrations: Taylor 1960: pl. 47: fig. 3, pl. 48: fig. 1; Littler and Littler 2000: 23; Braune and Guiry 2011: fig. 125.3; Cormaci et al. 2017: FP223, figs. 3, 4.]

Amphiroa tribulus (J.Ellis et Sol.) J.V.Lamour.

FIGURE 13

Amphiroa tribulus (J.Ellis et Sol.) J.V.Lamour. 1816: 302.

Basionym: *Corallina tribulus* J.Ellis et Sol. 1786: 124, pl. 21e.

Puerto Rican Records: Howe 1915; Almodóvar and Blomquist 1959; Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a; Bailey et al. 2004; Ballantine et al. 2016b.

Western Atlantic Distribution: Panama, United States (Florida, Texas), Bahamas, Cuba, Florida, Guadeloupe, Hispaniola,

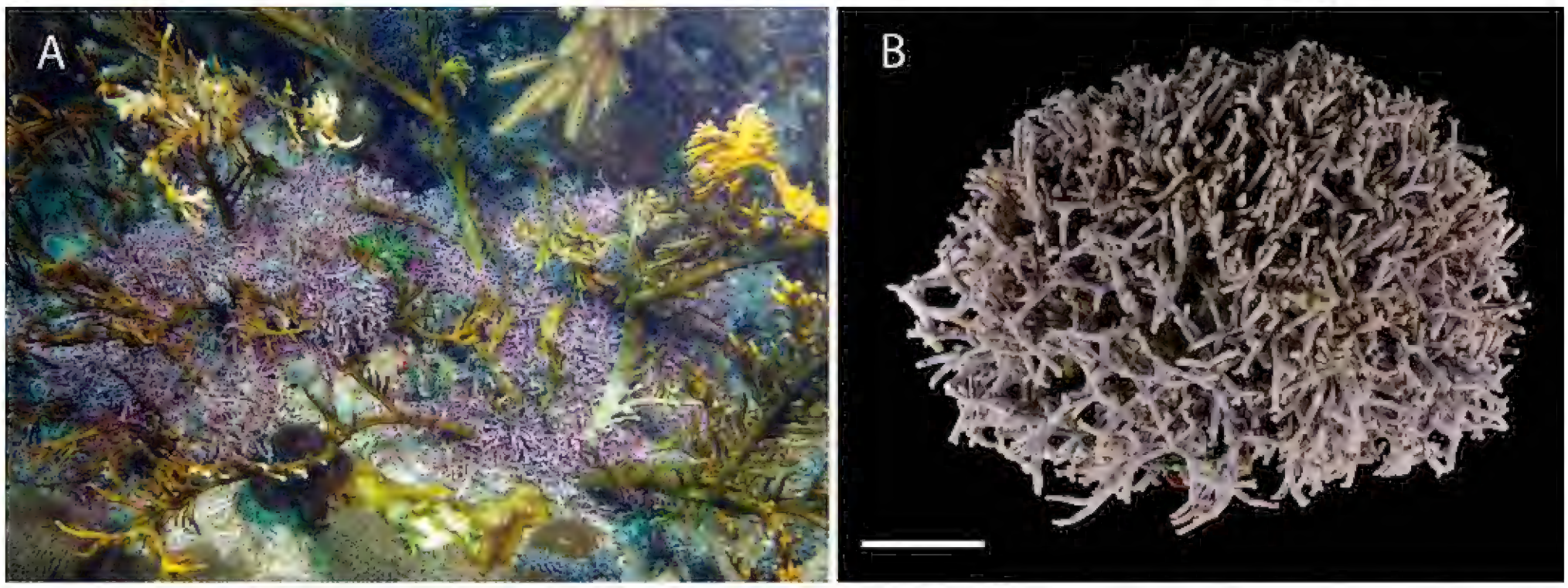

FIGURE 12. *Amphiroa rigida*. (A) In situ photograph, San Cristobal Reef, La Parguera, 2 m, growing at the base of a *Millepora alcicornis* L. colony. Field width = approximately 0.3 m. (B) DLBsn, herbarium specimen, San Cristobal Reef, La Parguera, 1.5 m. Scale bar = 2.0 cm.

FIGURE 13. *Amphiroa tribulus*. In situ habit photograph, algal plain, offshore from Margarita Reef, La Parguera, 17 m. Field width = approximately 10 cm.

Honduras, Jamaica, Martinique, Puerto Rico, St. Eustatius, Trinidad and Tobago.

World Distribution: See Guiry and Guiry 2024.

Type Locality: "West-Indian islands."

Lectotype: Ellis and Solander's (1786: pl. 21e) original illustration.

Epitype: Dieppe Bay, St. Kitts-Nevis (Woelkerling and Harvey 2012: 113).

Heavily calcified thalli occur in closely branched clumps, to 10 cm in extent. Axes are widely di–trichotomously, polychotomously, or irregularly branched. Segments are brittle and irregular in shape, more or less terete proximally but becoming flattened or triangular at mid-thallus and distally. The flattened segments, 2.0–4.0 mm broad and to 12 mm long, may become costate. The distal segments are tapered or acute. Segment medullary construction consists of 4–8 arching tiers of longer cells, 60–70 µm, that alternate with a single layer of shorter cells, to 30 µm long. A thick cortex of small cortical cells surrounds the medullary core. The genicula possess 3–6 tiers of cells. Tetrasporangial conceptacles are scattered over segment surfaces, measuring 205–280 mm diam. and 90–130 mm high.

Habitat and Comments: *Amphiroa tribulus* is frequently associated with shallow to 10 m deep coral reef habitats. [Additional illustrations: Littler and Littler 2000: 25; Braune and Guiry 2011: fig. 125.5; Harvey et al. 2013: figs. 36–39.]

Excluded Taxon

***Amphiroa beauvoisii* J.V.Lamour. 1816: 299.**

Almodóvar and Ballantine (1983) incorrectly added *A. beauvoisii* to the Puerto Rican flora.

DERMATOLITHEAE J.CABIOCH

Titanoderma Nägeli

Titanoderma Nägeli in Nägeli and C.E. Cramer 1858: 532.

Thalli are encrusting to foliose, lacking perithallial protuberances, and reach 3.0 cm in extent. They are fragile, weakly adherent, and grow mainly as epiphytes, epizoically and rarely epilithically. The hypothallus is a single basal layer of sinuate cells ("laughing cells" sensu Foslie, 1904a: 3), supporting an upright perithallus at ± right angles (heterotrichous organization or "dimerous" sensu Woelkerling 1988: 7, 227). The perithallus is relatively thin, composed of up to 12(–20) stratified layers of palisade cells. Adjacent hypothallial or perithallial cells are pit connected, whereas cell fusions and trichocytes are rare. Conceptacles are uniporate and can be raised or immersed in the perithallus. Reproductive characters are similar to other Lithophyllaceae. Spermatangial structures are simple and restricted to the chamber floor, whereas carposporangia develop from the periphery of a central fusion cell. Tetra/bisporangial conceptacles possess a central filamentous columella. Older conceptacles may become embedded in the perithallus.

Although Campbell and Woelkerling (1990) and Woelkerling and Campbell (1992) treated *Titanoderma* as a synonym of *Lithophyllum*, most later authors retain *Titanoderma* and *Lithophyllum* as two distinct genera (e.g., Chamberlain and Irvine 1994a; Athanasiadis 1996, 2016; Schneider and Wynne 2007; Baba and Kato 2023). Moreover, saxicolous species of *Titanoderma* with a larger thallus (>3 cm) forming erect perithallial protuberances are segregated in the genus *Goniolithon* (Foslie 1898: 5; Cabioch 1972: 210; Athanasiadis 2016: 300). At least 10 species of *Titanoderma* are recognized worldwide, of which the generitype occurs in Puerto Rico.

Titanoderma pustulatum (J.V.Lamour.) Nägeli

Titanoderma pustulatum (J.V.Lamour.) Nägeli in Nägeli and C.E.Cramer 1858: 532, footnote.

Basionym: *Melobesia pustulata* J.V.Lamour. 1816: 315, pl. 12: fig. 2.

Homotypic Synonym: Lithophyllum pustulatum (J.V.Lamour.) Foslie 1904a: 8.

Puerto Rican Records: Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Belize, Caribbean Mexico, Panama, United States (Florida, North Carolina, Texas), Bermuda, Barbados, Cuba, Guadeloupe, Hispaniola, Martinique, Panama, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: ["Côtes de France"], northern France (Lamouroux 1816).

Thalli are moderately calcified, fragile, suborbicular crusts that are completely attached across the entire ventral surface and measure 2.0–10 mm in extent. The hypothallus consists of a single layer of cells frequently taller than broad and is typically sinuate, 10–15 µm diam. and 12–55 µm high. The perithallus consists of palisade cells of about similar size. The crusts are mostly 2 cells thick but become superposed, resulting in the entire thallus being

2–3(–8) cells and to 350 µm thick. A single-layered epithallus of lenticular cover cells, 8.0–15 µm diam., terminates perithallial filaments. Shallowly conical female conceptacles measure to 500 µm diam. Tetrasporangial and bisporangial conceptacles, 300–500 µm diam., are hemispherical. Tetrasporangia are 22–70 µm diam. and 55–130 µm long. Algae are pink to whitish in color.

Habitat and Comments: *Titanoderma pustulatum* is most commonly collected as an epiphyte in shallow-water habitats. It is presently recognized as a cosmopolitan species. Depending on conceptacle size and shape, roof structure, and perithallus thickness, four distinct varieties are recognized in the British Isles (Chamberlain 1991), which are considered to be distinct species by some authors (Chamberlain 1986; Price et al. 1986; Boudouresque and Perret-Boudouresque 1987; Athanasiadis 2016). [Illustrations: Schneider and Searles 1991: figs. 287–291; Chamberlain and Irvine 1994a: figs. 38–40; as *Lithophyllum pustulatum*, Woelkerling and Campbell 1992: figs. 50–60.]

Lithophylleae Zanardini

Lithophyllum R.A.Phil.

Lithophyllum R.A.Phil. 1837: 387.

Thalli are encrusting, either lacking protuberances or with extensive perithallial proliferations that may dominate over the encrusting base. Unattached thalli form rhodoliths. Thallus organization is heterotrichous ("dimerous" sensu Woelkerling 1988: 7, 227), composed of a monostromatic hypothallus supporting an upright perithallus at ± right angles. The perithallus may secondarily become decumbent ("faux hypothalle" [false hypothallus] sensu Cabioch 1972: pl. 4: figs. 3, 4, 1988: figs. 5G, 6D; Athanasiadis 1999b: figs. 6, 11). Hypothallial cells are of various shapes, usually squarish or palisade. Perithallial cells may show stratification and comprise squarish or rectangular cells that possess secondary pit connections between adjacent cells; cell fusions are absent. One to 4 flattened epithallial cells terminate perithallial filaments. Trichocytes are not reported in Caribbean species but are described in congeners from the Indo-Pacific and South Atlantic. Conceptacles are slightly raised or flush with the surface and usually become embedded in the perithallus (or senesce in certain species). Spermatangial conceptacles develop simple spermatangia on the chamber floor. Carposporangial conceptacles develop carposporangia from the periphery of a central fusion cell. Tetrasporangial and bisporangial conceptacles sometimes possess a central calcified or filamentous columella, and ostioles can be flush with the surface or distinctively sunken. *Lithophyllum* is a large genus with some 125 species recognized worldwide. Five of these species, including the generitype *L. incrustans*, are known to Puerto Rico.

KEY TO THE *LITHOPHYLLUM* SPECIES OF PUERTO RICO

1. Thalli lacking a perithallus . . . . . *L. prototypum*
   Thalli with a perithallus 2
2. Thalli with extensive erect perithallial protuberances 3
   Thalli lacking erect perithallial protuberances 4
3. Apical branches confluent (irregularly anastomosing) . . . . . *L. congestum*
   Apical branches lamellate . . . . . *L. daedaleum*
4. Perithallus lacking cell stratification . . . . . *L. intermedium*
   Perithallus with cell stratification . . . . . *L. incrustans*

Lithophyllum congestum (Foslie) Foslie

FIGURE 14

Lithophyllum congestum (Foslie) Foslie 1900b: 20.

Basionym: Goniolithon congestum Foslie 1899: 13.

Puerto Rican Records: Steneck and Adey 1976; Ballantine and Aponte 2002a; Ballantine et al. 2004: figs. 2, 3.

Western Atlantic Distribution: Colombia, Caribbean Mexico, Puerto Rico, Brazil, St. Bartholomew.

Type Locality: St. Bartholomew.

Thalli form complexes to 16 cm in extent that are attached to rocks or corals by a basal crust, 1.0 mm thick, producing a hemispherical frond to 9.0 cm tall. The erect branches are terete or sub-compressed proximally, 1.0–2.0 mm thick, becoming irregularly divided, confluent, and closely arranged. The outer lobes are frequently more compressed, irregularly confluent, 3.0–8.0 mm broad and about 1.0 mm thick. Distal branches are blunt and folded or twisted and anastomosing at the summit. New crusts are formed from branches becoming decumbent and attaching to the substratum. Sporangial conceptacles occur on the outer branches and are crowded, convex to subconical but not sharply defined, measuring ~300 µm diam., with a central pore and about 20 delicate and indistinct lateral pores. Bisporangia are 55–75 µm broad and 80–100 µm long.

Habitat and Comments: Steneck and Adey (1976) credited *L. congestum* as being the primary framework builder of some Caribbean coral ridges. The species achieves its maximum development in shallow water with high levels of turbulence and light, where it may attain an apical branch extension of 8.0 mm/yr and a marginal extension of greater than 10.8 mm/yr.

Littler and Littler (2000) also reported the species to be abundant in shallow-water, wave-impacted coral reefs. Ballantine

et al. (2004) reported smaller colonies (to 4.5 cm tall) than those described in the protologue (cited above).

According to Woelkerling (1993: 59), the original material in TRH comprises five specimens, two of which are illustrated by Printz (1929: pl. 66: figs. 6, 7). Tâmega et al. (2014: figs. 2, 7, 8) and Hernandez-Kantun et al. (2016: figs. 3–5) examined four type specimens (three in TRH, one in NY) but failed to give a coherent description with illustrations of the internal structure regarding the hypothallus, size of vegetative cells, and the apparent lack of trichocytes or to clarify the peculiar description of the ostiole(?) structure in the protologue. Tâmega et al. (2014: figs. 7, 8) showed instead a perithallial branch with stratified internal growth supporting a series of superficial empty uniporate conceptacles, known to occur in lamellate species of the genus (Woelkerling 1988: fig. 76; Riosmena-Rodriguez et al. 1999: fig. 4), and finally, both research groups considered *L. congestum* to be a synonym of other species.

FIGURE 14. *Lithophyllum congestum*. Reef front, Media Luna Reef, 1.0 m. Scale bar = 1.0 cm.

In particular, Hernandez-Kantun et al. (2016: 621, 625, 627) reported that partial *rbc*L sequences (263–309 base pairs [bp]) from type specimens of *L. congestum* (TRH A23-1381), *L. daedaleum* (NY 00945458), and *L. kaiseri* (Heydr.) Heydr. (NY 00945463) are identical and proposed conspecificity between them with the name *L. kaiseri* as having priority. We have been critical before of making taxonomic conclusions based on partial type sequences alone, without comparison to newly collected topotypes (Athanasiadis 2020; Athanasiadis and Ballantine 2024). Moreover, our interpretation of Hernandez-Kantun et al.'s (2016: 625, US Alg. Coll. 170945) fig. 9, said to be of a Caribbean specimen of "*L. kaiseri* with a "monomerous" hypothallus, is that the figure shows numerous cell fusions but no secondary pit connections and hence the material cannot belong to Lithophyllaceae. It also appears that the type of *L. kaiseri* from the Red Sea develops numerous trichocytes in vertical series (Basso et al. 2015: fig. 5 B, D), a character both absent from the protologue of *L. congestum* and lacking in all Puerto Rican species of *Lithophyllum*. According to the protologue, the original material of *G. congestum* was deposited in the Swedish Museum of Natural History of Stockholm (S) and was collected at St. Bartholomew by the Swedish government official Axel Theodor von Goes. [Additional illustrations: Printz 1929: pl. 66: figs. 6, 7; Littler and Littler 2000: 35; Ballantine et al. 2004: figs. 2, 3; Tâmega et al. 2014: figs. 2, 7, 8; as a synonym of *L. stictiforme*, Hernandez-Kantun et al. 2016: figs. 3–5; as a synonym of *L. kaiseri*, Hernandez-Kantun et al. 2016: figs. 3–5.]

Lithophyllum daedaleum Foslie et M.Howe

Lithophyllum daedaleum Foslie et M.Howe 1906a: 133, pls. 83, 84, 93.
Puerto Rican Records: Printz 1929; Taylor 1960; Ballantine and Aponte 1997a.
Western Atlantic Distribution: Caribbean Mexico, Puerto Rico, Trinidad, U.S. Virgin Islands.
Type Locality: Salinas Bay, near Guánica, Puerto Rico.

Thalli are firmly attached to the substratum by a primary crust, 0.5–2.0 mm thick, that issues crowded, repeatedly subdichotomous, and anastomosing branches about 2.0 mm thick, with roundish, truncate or, more frequently, lobate apices that are depressed in the center. The erect thallus reaches 6.0 cm in height, with apical parts being fused and molariform-daedaleoid, 3–15 mm broad. Perithallial cells are 8.0–14 µm broad and 8.0–36 µm long and do not show stratification (Foslie and Howe 1906a: pl. 93). Epithallial cells measure 4.0–12 µm diam. Sporangial conceptacles are convex, ~300 µm diam. Unattached specimens (rhodoliths) have not been seen. Reproductive features and distributional data were given by Foslie (1909: 37) as follows: Tetrasporangial conceptacles are convex and slightly prominent, 225–380 µm in diam., with tetrasporangia 60 µm long and 30–35 µm diam. Carposporangial conceptacles are convex-conical but slightly prominent, ~200–350 µm diam. (seen from above). Male conceptacles were not seen.

Habitat and Comments: *Lithophyllum daedaleum* is widely distributed in the West Indies. According to Foslie (1909: 37), a BM specimen from Trinidad was previously referred to *L. pallescens* (Foslie) Foslie. *Lithophyllum daedaleum* also occurs on Margarita Island (Venezuela), whereas a few poorly developed specimens from Brazil (locality unknown) seem to belong to the same species (Foslie 1909). *Lithophyllum daedaleum* was originally collected on exposed rocks near the low-water mark. Four collections, all from Puerto Rico, were cited in the protologue, and a "type" was designated and illustrated (Foslie and Howe 1906a: pl. 83, Howe no. 2676). Their pl. 83 shows images of two specimens (one in two views) reaching 6.0 and 12 cm, respectively. Adey and Lebednik (1967: 22) selected as lectotype a specimen from Salinas Bay in TRH (A22-1337) that according to Woelkerling (1993: 70) and Woelkerling et al. (2005: 181), is illustrated by Printz (1929: pl. 66: fig. 2) and is, indeed, annotated "2676."

Lithophyllum daedaleum has also been reported from the harbor of Christiansted, St. Croix (Lemoine in Børgesen 1917: 162–163, fig. 158) and also as a synonym of *L. congestum* from Colombia (Díaz-Pulido and Díaz-Ruíz 2003). However, studies of its structure and reproduction are lacking, whereas the type of the sporangial conceptacles described in the protologue remains unknown. Hernandez-Kantun et al. (2016: 621, 625, 627) reported that partial *rbc*L sequences (263–309 bp) from type specimens of *L. congestum* (TRH A23-1381), *L. daedaleum* (NY 00945458), and *L. kaiseri* Heydr. (NY 00945463) are identical and proposed conspecificity, recognizing *L. kaiseri* as the correct species name, a species originally described from the Red Sea (see Basso et al. 2015).

Specimens collected by Howe from Salinas Bay, San Juan, Culebra, and Guánica are deposited in the Foslie herbarium (Adey and Lebednik 1967). [Illustrations: Foslie and Howe 1906a: 133, pls. 83, 84, 93; Printz 1929: pl. 66: figs. 1–4.]

Lithophyllum daedaleum var. *pseudodentatum* Foslie et M.Howe

Lithophyllum daedaleum var. *pseudodentatum* Foslie et M.Howe 1906a: 133–134, pl. 85: fig. 1.
Western Atlantic Distribution: Caribbean Mexico, Puerto Rico.
Type Locality: Salinas Bay, near Guánica, Puerto Rico.

Thalli differing from the autonym in having many of the branches broadened distally, plano-compressed, or subflabelliform, the branches sometimes attaining a width (including anastomoses) of 2.0 cm.

Habitat and Comments: This variety was collected on surf-beaten rocks in the low littoral. A single specimen (Howe no. 2675) ~10.5 cm in extent was illustrated in the protologue. The TRH material comprises a second specimen ~7.5 cm in extent from the same collection (Howe no. 2675; Printz 1929: pl. 66: fig. 5). The lamellate protuberances of var. *pseudodentatum* resemble those of the Mediterranean *L. dentatum* (Kütz.) Foslie, but no comparative information on the internal structure or reproduction of var. *pseudodentatum* exists. A single later record from Isla Verde, Veracruz, Mexico, has been published (Mateo-Cid et al. 1996). [Illustrations: Foslie and Howe 1906a: pl. 85: fig. 1; Printz 1929: pl. 66: fig. 5.]

Lithophyllum incrustans R.A.Phil.

FIGURE 15
Lithophyllum incrustans R.A.Phil. 1837: 388.
Puerto Rican Records: Ballantine et al. 2011.
Western Atlantic Distribution: United States (Florida, North Carolina), Barbados, Jamaica, Puerto Rico, U.S. Virgin Islands.
Type Locality: Sicily, Mediterranean Sea.

Thalli are thick, to 1.1 mm, and at least 10 cm in extent and lack erect perithallial protuberances. Thalli have a distinctive growth in that elevated ridges are formed where adjacent thalli meet and grow together. The hypothallus is unilayered, composed of squarish to trapezoid or rectangular cells, 12–18 µm long and 9.0–12 µm broad. Each hypothallial cell produces a dorsal arching perithallial filament composed of cells 5.0–17 µm long and 7.0–11 µm broad. Cells of perithallial filaments show a more or less stratification and terminate in single epithallial cells that are rectangular or flattened, 8.0–9.0 mm diam. and 2.0–3.0 mm long (see Figure 15). Figure 15 illustrates the morpho-anatomy of *L. incrustans* in Puerto Rican material reported by Ballantine et al. (2011). Gametangial thalli are dioecious, and the conceptacles protrude slightly above the thallus surface. Male conceptacles are 210–270 µm in external diameter and up to 38 µm high. Carposporangial conceptacles are 380–400 µm in external diameter and 40–52 µm high. Carposporangia measure 30–50 µm diam. Tetrasporangial conceptacles are flush with the crust surface or project up to 50 µm, with a diameter of 350–420 µm. Tetrasporangia are 45–80 µm long and 20–30 µm broad. Older conceptacles become embedded in the perithallus. Algae are dull chalky yellowish or pink in color.

Habitat and Comments: Puerto Rican specimens are epizoic on dead *Lobatus gigas* (L.) shells in shallow water. *Lithophyllum incrustans* was designated as the generitype by Foslie (1898: 5, 6), who distinguished the genus *Lithophyllum* from *Lithothamnion* on the basis of its uniporate tetrasporangial conceptacles. The lectotype material of *L. incrustans* was studied by Woelkerling (1983: figs. 15–21), who showed that it is attached to a gastropod shell and its thallus develops a monostromatic hypothallus supporting an erect stratified perithallus. Richards et al. (2018) recently reinstated *L. intermedium* and *L. subtenellum* (Foslie) Foslie and also described a new species of *Lithophyllum*, *L. searlesii* Gabrielson, Freshwater, J.Richards et Hughey, from North Carolina. This group of three species differs vegetatively from *L. incrustans* in lacking both perithallial cell stratification and decumbent perithallial proliferations ("faux hypothalle" sensu Cabioch (1972: pl. 4: figs. 3, 4; 1988: figs. 5G, 6D; see also Athanasiadis 1999b: figs. 11–12). In light of the recent recognition of *L. searlesii* and *L. intermedium* in the western Atlantic (Richards et al. 2018), most Caribbean

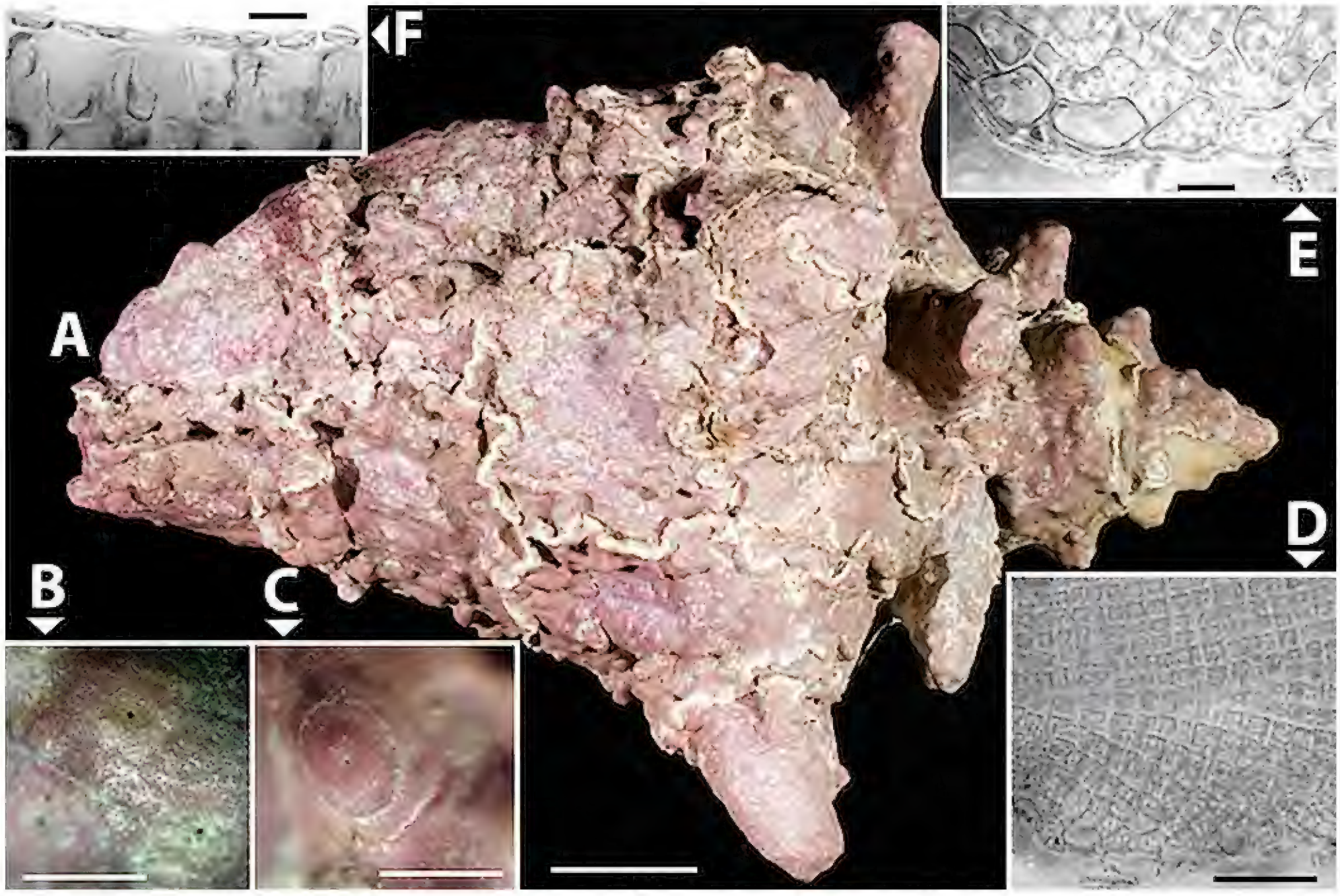

FIGURE 15. *Lithophyllum incrustans*. (A) DLB7783, growing on a *Lobatus gigas* shell, La Parguera, 1.0 m. Scale bar = 2.0 cm. (B, C) AAPR-27, uniporate conceptacles. Scale bars = 350 µm. (D) AAPR-27, thallus section showing stratified perithallus. Scale bar = 50 µm. (E, F) AAPR-27, epithallial and hypothallial cells, respectively. Scale bars = 10 µm.

records of *L. incrustans* require confirmation. [Additional illustrations: Woelkerling 1983: figs. 15–21; Braune and Guiry 2011: fig. 133.1; Cormaci et al. 2017: FP248, figs. 1, 2.]

Lithophyllum intermedium Foslie

Lithophyllum intermedium Foslie 1906b: 23.

Misapplied Name: *Lithothamnion intermedium* Kjellm. 1883: 127, pl. 4: figs. 1–10.

Puerto Rican Records: Foslie 1906b, with reservation; Børgesen 1917; Taylor 1960. As *Lithothamnion intermedium*: Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida, North Carolina), Bermuda, Barbados, Jamaica, Puerto Rico, U.S. Virgin Islands.

Syntype Localities: Florida ("Exp. W[u]rdemann"); Jamaica ("herb. Collins"); St. John, U.S. Virgin Islands ("Børgesen"); Barbados ("Lassen, comm. Borgesen"); and San Juan, Puerto Rico (Foslie 1906a).

Lectotype Locality: St. John, U.S. Virgin Islands (Adey and Lebednik 1967: 21).

Thalli are encrusting, up to 3.0 mm thick, with a smooth, glossy surface, becoming mammillate as a result of conformation to the substratum underneath and with crenulate or irregularly lobed margins. The hypothallus is single layered, with cells measuring 6.0–15 µm broad and 5.0–25 µm long. The perithallus consists of cells that measure 5.3–11 µm broad and 7.2–22 µm long. Neither perithallial stratification nor decumbent perithallial proliferations are known. Secondary pit connections occur between adjacent vegetative cells, whereas trichocytes and cell fusions are lacking. The epithallus is composed of 1 or 2 cells, 3.0–4.0 µm long and 6.0–8.8 µm diam. Putative tetrasporangial conceptacles are uniporate, 150–300 µm diam., and slightly elevated.

Habitat and Comments: From specimens of the syntype localities, Adey and Lebednik (1967: 21) selected as lectotype the material from St. John (Printz 1929: pl. 57: figs. 7, 8) and several slides (see Woelkerling et al. 2005: 55, TRH A6-275). Adey (1970: 5) narrowed the lectotype to "the one . . . sectioned and

appears in the Monograph." From the lectotype collection, Richards et al. (2018: 321, figs. 4–9) selected a specimen of *Lithophyllum* that lacks perithallial stratification and decumbent branches, but they did not examine the slides that were explicitly selected as part of the lectotype (Adey 1970: 5).

Lithophyllum intermedium is apparently associated with coral reefs and other encrusting coralline algae, but its habitat and ecology remain to be studied. Our account above is based on data from the protologue and the lectotype as described by Richards et al. (2018). A thorough investigation of the entire type material in TRH remains to be published. It should be added that the illustration published by Lemoine in Børgesen (1917: 161–162, fig. 157), which is based on collections from the type locality ("St. Jan: Cruz Bay, No 2196; Great Cruz Bay près de la côte No.1783, 1782"), shows apparent perithallial stratification, which occurs in *L. incrustans*. Specimens collected by Howe (no. 2346) from San Juan and deposited in the Foslie herbarium (Adey and Lebednik 1967) are referred to this species with reservation (Foslie 1906b). [Illustrations: Printz 1929: pl. 57: figs. 7, 8; Richards et al. 2018: figs. 4–9.]

Lithophyllum prototypum (Foslie) Foslie

FIGURE 16

Lithophyllum prototypum (Foslie) Foslie 1905c: 129.

Basionym: *Lithothamnion prototypum* Foslie 1897: 18.

Homotypic Synonym: Titanoderma prototypum (Foslie) Woelk., Y.M.Chamb. et P.C.Silva 1985: 333.

Puerto Rican Records: Howe 1920b; Taylor 1960; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Bahamas, Bermuda, Jamaica, Puerto Rico, U.S. Virgin Islands.

World Distribution: See Guiry and Guiry 2024.

Type Locality: St. Croix, U.S. Virgin Islands.

Encrusting thalli, reach 2.0–5.0 cm diam. or greater in extent and 0.1–0.9 mm thick, becoming regularly superposed by new branches growing in a spiraling pattern. Individual lamellae are up to 350 µm thick and possess thin margins that are free from the substratum. Some specimens possess small outgrowths. Palisade hypothallial cells, 10–15 µm long and 15–50 µm high, form secondary pit connections between cells of adjacent filaments. Neither cell fusions nor trichocytes occur. A perithallus is lacking. Epithallial cells are squarish to rounded and measure 10–15 µm in diam. and 1.5–3.0 µm long. Gametophytes are dioecious. Spermatangial conceptacles measure 135–185 µm in diam. and 37–60 µm high. Carposporangial conceptacles are partially embedded, 450–670(–740) µm diam. and 100–150 µm high. Tetrasporangial conceptacles are subconical and protrude, measuring to 400 µm diam.

Habitat and Comments: *Lithophyllum prototypum* is principally epiphytic, particularly on *Rhizophora mangle* L.; epizoic on shells; or epilithic on stones, typically in shallow-water reef environments. This species differs from all other members of the genus *Lithophyllum* by its unique thallus organization, that is, a regular superposition of new branches in spirals, each composed of 2 cell layers: a hypothallus and an epithallus. Specimens collected by Howe from Culebra and San Juan are deposited in the Foslie herbarium (Adey and Lebednik 1967). [Additional illustrations: as *Lithophyllum prototypum*, Lemoine in Børgesen 1917: figs. 163, 164; Woelkerling and Campbell 1992: figs. 42–49; as *Titanoderma prototypum*, Littler et al. 1989: 219; Littler and Littler 2000: 41.]

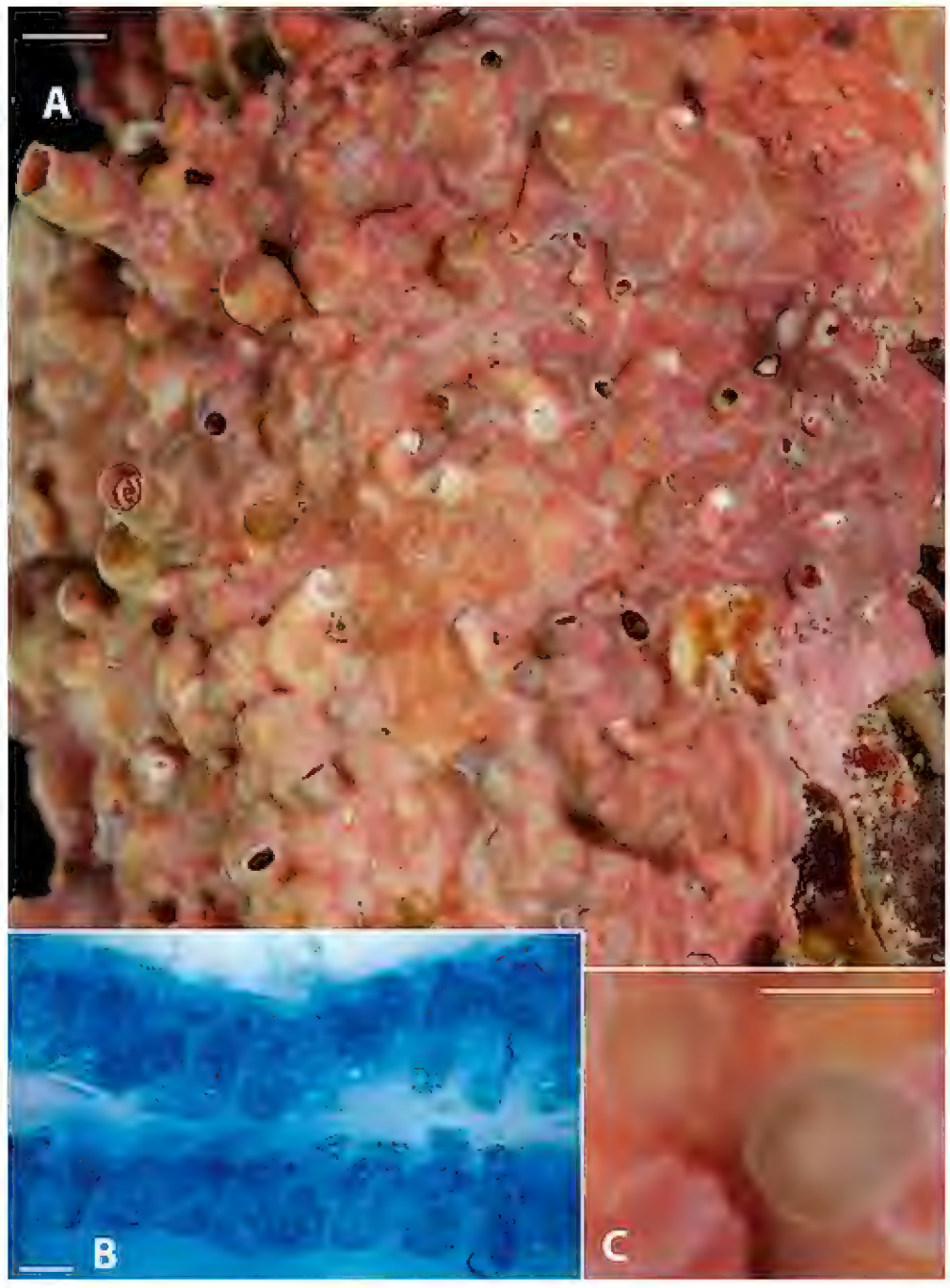

FIGURE 16. *Lithophyllum prototypum*. (A) HRsn, live specimen, La Parguera, sublittoral. Scale bar = 1.0 cm. (B) AAPR-42, thallus section of two branches in superimposition, Collado Islet, La Parguera, 0.2–0.3 m, on mangrove root. Scale bar = 10 µm. (C) HRsn, two conceptacles. Scale bar = 500 µm.

Lithothamnionaceae Athanas. et D.L.Ballant.

Lithothamnieae Foslie

Lithothamnion Heydr.

Lithothamnion Heydr. 1897a: 412, nom. cons.

Thalli are primarily encrusting and may produce erect perithallial protuberances. They occur epiphytically, epizoically,

epilithically, or as rhodoliths. The encrusting thallus is composed of a polystromatic, non-coaxial hypothallus supporting a gradually ascending perithallus, terminating in a layer of flared epithallial cells. Subepithallial meristematic cells are elongate prior to division. Cell fusions occur between adjacent vegetative cells, and secondary pit connections are absent. Trichocytes are absent in the well-known species. Gametophytes are dioecious with uniporate conceptacles. Spermatangia are dendroid (branched) structures and develop on the floor, the walls, and the roof of the chamber. Carposporangia develop across the fertile floor after individual fertilization. Tetrasporangial and bisporangial conceptacles are multiporate. Pore cells lining the canals are usually not differentiated. This is a large genus, not revised in most parts of the world, with some 77 species currently recognized (Guiry and Guiry 2024), 3 of which occur in Puerto Rico.

KEY TO THE *LITHOTHAMNION* SPECIES OF PUERTO RICO

1. Thalli develop conceptacles in series that form erect protuberances . . . . . *L. carpoklonion*
   Thalli develop conceptacles spread on the thallus. 2
2. Branch tips are fluted . . . . . *L. ruptile*
   Branch tips are blunt or with shallow cavities . . . . . *L. occidentale*

Lithothamnion carpoklonion Athanas. et D.L.Ballant.

FIGURE 17

Lithothamnion carpoklonion Athanas. et D.L.Ballant. 2011: 403, figs. 1–21.
Puerto Rican Records: Athanasiadis and Ballantine 2011.
Western Atlantic Distribution: Puerto Rico.
Type Locality: Collado Reef, La Parguera, Puerto Rico.

Crustose to foliaceous thalli measure to 10 cm in extent and 370 µm thick. The hypothallus is non-coaxial and composed of 2–4 layers with cells 13–34 µm in length. Perithallial cells are smaller, and the hyaline terminal epithallial cells are flared. Erect protuberances, 1.0–2.0 mm long and ~0.5 mm broad, are formed by series of tetrasporangial or gametangial conceptacles. Gametangial conceptacles are conical to ovate. Male conceptacles measure 600 µm diam. and are 350–380 µm high. Carposporangial conceptacles measure 650–750 µm diam. and are 350–450 mm high. Tetrasporangial conceptacles measure 365–580 µm diam. and are to 190 µm high. The roof of mature tetrasporangial conceptacles is convex, possessing at least 70 pores, and the pore cells lining the canals are non-differentiated. Tetrasporangia measure 30–52 mm diam. and 85–142 mm long. Algae are violet or reddish in color.

Habitat and Comments: *Lithothamnion carpoklonion* is currently only known in Puerto Rico on the islets at Collado and Enrique Reefs in the inner reef arc off the coast of La Parguera. This endemic species is an epiphyte on prop roots of *Rhizophora mangle* growing in association with *Magnephycus ornatus* and other encrusting corallines, just below water level in shaded, sheltered habitats of these islets. [Additional illustrations: Athanasiadis and Ballantine 2011: figs. 1–21.]

FIGURE 17. *Lithothamnion carpoklonion.* DLB8273, live specimen, La Pelotas Reef, La Parguera, 0.1 m, epiphytic on *Rhizophora.* Scale bar = 1.0 mm.

Lithothamnion occidentale (Foslie) Foslie

FIGURE 18

Lithothamnion occidentale (Foslie) Foslie 1908b: 3.
Basionym: *Lithothamnion fruticulosum* f. *occidentale* Foslie 1906b: 12 (as f. "*occidentalis*").
Puerto Rican Records: Ballantine et al. 2004.
Western Atlantic Distribution: Caribbean Mexico, United States (Florida, North Carolina, South Carolina), Bermuda, Cuba, Hispaniola, Martinique, U.S. Virgin Islands, Puerto Rico, Brazil, Venezuela.
Type Locality: Off Cruz Bay, St. John, U.S. Virgin Islands.

Thalli are irregularly branched and free-living. Individual rhodoliths reach up to 5.0 cm diam. and up to 3.0 cm in height. Branches are short and terete to compressed, 1.5–3.0 mm diam., and these sometimes anastomose. The branch apices are blunt or bear typical shallow cavities. The perithallus consists of rectangular or slightly swollen cells, 6.0–10 µm diam. and 10–32 µm long. Cells of adjacent perithallial filaments may fuse. Secondary pit connections and trichocytes are absent. A single-layered epithallus consists of cells 8.0–12 µm diam. and 5.0–7.0 µm high. Tetrasporangial conceptacles are inconspicuous, and tetrasporangia measure 75 µm diam. and 180 µm long. Algae are pink in color.

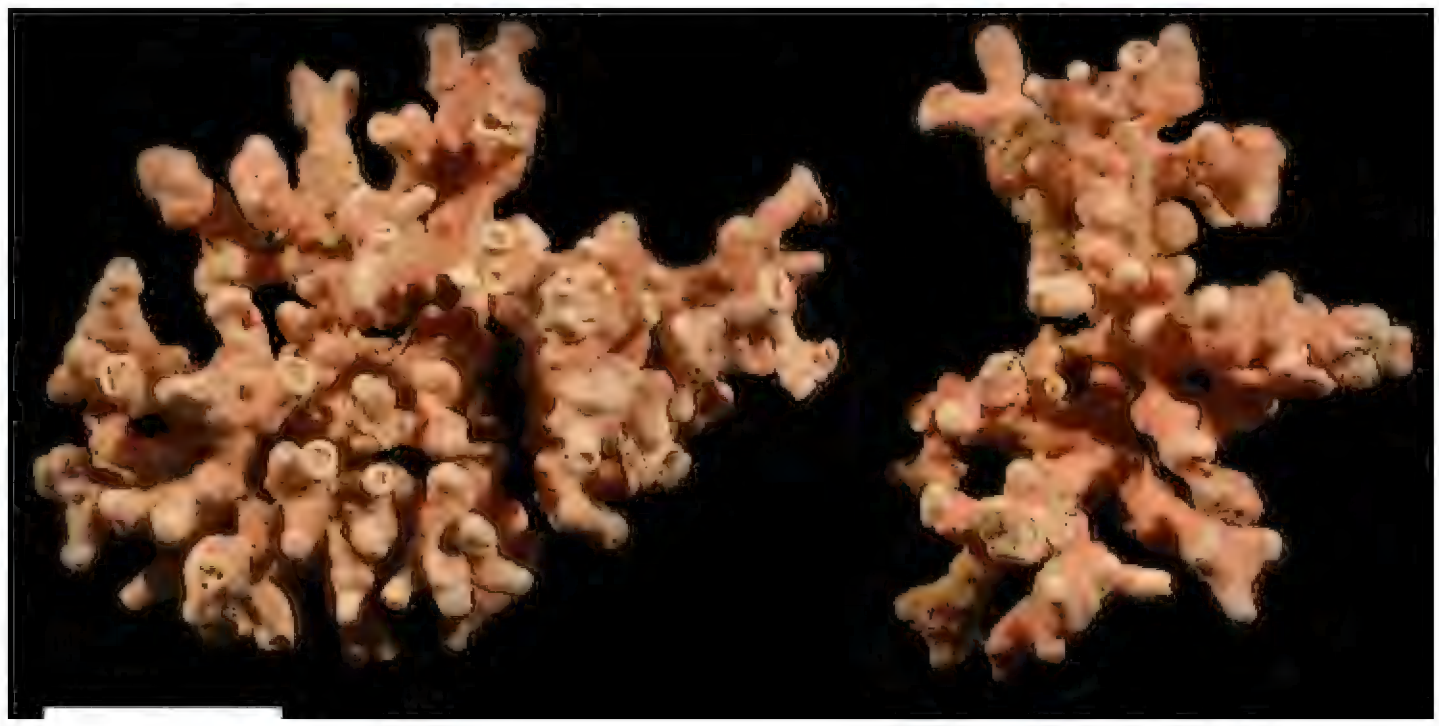

FIGURE 18. *Lithothamnion occidentale*. DLB2348, habit of two specimens, algal plain seaward of Margarita Reef, 24 m. Scale bar = 1.0 cm.

Habitat and Comments: *Lithothamnion occidentale* has been collected growing unattached in the southern Puerto Rico algal plains. Despite several literature reports, a study of the original material has not been undertaken. Adey (1970: 21) noted the presence of several specimens in the original material but provided no specific details. Collections from two (syn)type localities were cited in the protologue, and Woelkerling (1993) selected as lectotype a Børgesen collection of five specimens, two of which are illustrated by Printz[2] (1929: pl. 12: figs. 15, 17). These two specimens differ markedly in habit, the former resembling *Melyvonnea erubescens* (Athanasiadis and Ballantine 2014: 416), whereas the second one is a rhodolith, fitting our present account of *Lithothamnion occidentale*. The protologue describes the development of shallow cavities at the branch apices, resembling those of *L. ruptile* (Foslie 1907a). [Additional illustrations: Printz 1929: pl. 13: figs. 16–17; Taylor 1960: pl. 79: fig. 2; Ballantine et al. 2004: fig. 4.]

Lithothamnion ruptile (Foslie) Foslie

FIGURE 19

Lithothamnion ruptile (Foslie) Foslie 1907a: 5.

Basionym: *Lithothamnion syntrophicum* f. *ruptile* Foslie 1905a: 18 (as f. "*ruptilis*").

Puerto Rican Records: Ballantine et al. 2011.

Western Atlantic Distribution: Hispaniola, Puerto Rico, U.S. Virgin Islands.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Puerto Plata, Santo Domingo.

[2] Printz gathered Foslie's scattered notes including 30 plates and added 45 new ones, together with a list of Foslie's publications, an obituary, an account on the structure of coralline algae, an identification key to *Lithothamnion* species, a list of the illustrated species, and the explanation for all the plates.

Thalli are heavily calcified and brittle, nearly spherical colonies that are tightly branched, up to 8.0 cm in extent, and unattached. Branches are irregularly shaped and become free toward the surface of the colony and with broadly fluted branch apices. The hypothallus is 100–150 µm thick, producing an ascending perithallus 50–550 µm thick. Hypothallial cells are (15–)22–35 µm long and 5.0–15 µm broad, and perithallial cells measure 3.0–12 µm broad and 7.0–28 µm long. An epithallium is composed of a single layer of flared cells, 7.0–12 µm diam. and 2.0–4.0 µm long. Sporangial conceptacles measure 300–500 µm diam. and are slightly raised and multiporate. The tetrasporangia measure to 35 µm diam. and to 70 µm long. Algae are pink to red in color.

FIGURE 19. *Lithothamnion ruptile*. DLB6993, in situ habit photograph, algal plain, offshore from Punta Brea, Guánica, 17 m. Field = 10 cm.

Habitat and Comments: Puerto Rican *Lithothamnion ruptile* are unattached (rhodoliths) with tightly aggregated and anastomosing branches. Whereas Littler and Littler (2000) stated that the species was restricted exclusively to deep water (>30 m), Ballantine et al. (2011) reported the species from the Punta Brea algal plain at 17 m depth. The habit of *Lithothamnion ruptile* and its internal vegetative structure are similar to *Lithothamnion crispatum* Hauck described from the Adriatic Sea (cf. Cabioch and Mendoza 1998: figs. 28–31), and the two species may be conspecific or sister taxa, as previously suggested by Foslie (1905a) and Lemoine (in Børgesen 1917). Nevertheless, the reproductive structures remain to be compared between the two taxa before conspecificity can be proposed. [Additional illustrations: Littler and Littler 2000: 35; Ballantine et al. 2011: fig. 4.]

Melobesiaceae J.Früh

Melobesioideae Bizzozero

Melobesieae Aresch.

Melobesia J.V.Lamour.

Melobesia J.V.Lamour. 1812: 186.

Thalli are encrusting, adhering closely to macroalgae, pebbles, and rock. Thallus organization is heterotrichous ("dimerous" sensu Woelkerling 1988: 7, 227), composed of a monostromatic hypothallus giving rise to an erect perithallus of several cells terminating in single epithallial cells. Cells of adjacent filaments may fuse. Secondary pit connections and trichocytes are not formed. Conceptacles protrude slightly from the thallus surface. Spermatangia are simple and develop on the floor, the walls, and the roof of the chamber. Carposporangia are produced both laterally and orthostichously from gonimoblast filaments, whereas a conspicuous fusion cell is lacking. Tetrasporangial conceptacles are multiporate, and pore cells lining the canals have differentiated basal cells. The generitype, which is 1 of the 12 recognized *Melobesia* species, is known from Puerto Rico.

Melobesia membranacea (Esper) J.V.Lamour.

Melobesia membranacea (Esper) J.V.Lamour. 1812: 186.

Basionym: Corallina membranacea Esper 1796: pl. 12.

Homotypic Synonym: Epilithon membranaceum (Esper) Heydr. 1897a: 408.

Puerto Rican Records: Hauck 1888; Taylor 1960; Almodóvar 1964a, 1965; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002a. As *Epilithon membranaceum*: Almodóvar and Blomquist 1959.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Cuba, Guadeloupe, Hispaniola, Jamaica, Old Providence Island, Puerto Rico, Martinique, Panama, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Northern coast of France.

Lectotype: Esper's (1796: pl. 12) original illustration.

Epitype: Northern coast of France (Chamberlain 1985: 676–677; Woelkerling and Chamberlain 2007: 233).

Thalli are lightly calcified thin crusts, closely adhering to larger algae and seagrasses, and rarely occurring epilithically or epizoically. Thalli measure up to 5.0 cm in extent and to ~90 µm thick. In vertical section, hypothallial cells are squarish to palisade, 7.0–23 µm diam. (high) and 5.0–16 µm long. In vegetative thallus parts near the margin, hypothallial cells support a single layer of epithallial cells, with perithallial cells produced between the 2 layers in the main thallus and surrounding conceptacles. Gametangial conceptacles are to 250 µm diam., and tetrasporangial conceptacles are to ~280 µm diam. Following fertilization, the lower part of the carpogonium fuses with the hypogenous cell, and gonimoblast filaments develop radially at the level of hypogynous cells (Wilks and Woelkerling 1991: fig. 21). Carposporangia develop orthostichously and from the periphery of gonimoblast filaments (Athanasiadis and Ballantine 2024: fig. 80). Algae are reddish or white in color.

Habitat and Comments: *Melobesia membranacea* is commonly collected in Puerto Rico as an epiphyte on seagrasses and larger algae. Specimens collected by Howe from Aguadilla, Lemon Bay, Point Borinquen, and Santurce are deposited in the Foslie herbarium (Woelkerling et al. 2005: 119–120). Our species account is based in part on Chamberlain and Irvine (1994b: 196). [Illustrations: Wilks and Woelkerling 1991: figs. 1–22; Chamberlain and Irvine 1994b: figs. 93, 94; Borges et al. 2014: figs. 1–4; Athanasiadis and Ballantine 2024: fig. 80.]

Mesophyllaceae Athanas.

Mesophylloideae Athanas. et D.L.Ballant.

Magnephyceae Athanas. et D.L.Ballant.

Hyperandri Athanas. et D.L.Ballant.

Hyperandri Athanas. et D.L.Ballant. 2024: 106.

Thalli are saxicolous, epizoic, or epiphytic on the roots of *Rhizophora mangle*, reaching up to 4.0 cm in extent and strongly adhering to the substratum. Thallus organization is dorsiventral with a polystromatic, non-coaxial hypothallus supporting a gradually ascending non-stratified perithallus lacking protuberances. Subepithallial cells are longer than cells below and support single rectangular, flattened to roundish, or, rarely, flared epithallial cells. Cell fusions between contiguous vegetative cells are common, and secondary pit connections are absent. Terminal trichocytes may occur in thalli on specimens from the Canary Islands. Gametophytes are dioecious. Spermatangial structures occur on a centrally raised pedestal formed by a single layer of palisade cells, a character distinguishing the genus within the

Mesophyllaceae (Athanasiadis and Ballantine 2024: fig. 5l,m). Multiporate conceptacles have convex roofs, and the canals are straight and lined by filaments composed of cells that are thinner in radial section and broader in tangential section. Older conceptacles become embedded in the perithallus. The genus is distributed in the tropics and the subtropics, with three species recognized, one of which occurs in Puerto Rico.

Hyperandri bisporum (Foslie) Athanas. et D.L.Ballant.

FIGURE 20

Hyperandri bisporum (Foslie) Athanasiadis et D.L.Ballant. 2024: 106, figs. 37–41.

Basionym: *Lithothamnion bisporum* Foslie 1906a: 18.

Homotypic Synonyms: *Leptophytum bisporum* (Foslie) W.H.Adey 1970: 30; *Phymatolithon bisporum* (Foslie) Afonso-Carrillo 1984: 134.

Puerto Rican Records: Athanasiadis and Ballantine 2024. As *Leptophytum bisporum*: Athanasiadis and Ballantine 2014.

Western Atlantic Distribution: Bermuda, Puerto Rico.

World Distribution: Canary Islands (Athanasiadis and Ballantine 2024).

Type Locality: Tenerife, Canary Islands.

Thalli form irregular crusts up to 4.0 cm in extent and to 0.5 mm thick, via superimposition. Thallus organization is monopodial-dorsiventral with a polystromatic non-coaxial hypothallus, 70–100 µm thick, supporting an ascending non-stratified perithallus to 280 µm thick. Hypothallial cells are 12–25 µm long and 4.0–10 µm broad, and perithallial cells measure 6.0–15 µm long and 4.0–8.0 µm broad. Subepithallial cells are longer than cells below, to 8.0 µm long and 3.0 µm broad, supporting single epithallial cells that are flattened (to isodiametric-rounded), 2.0–3.0 µm long and 3.0–8.0 µm diam. Multiporate bisporangial conceptacles are convex, 180–500 µm diam., and perforated by canals that are straight and lined by filaments composed of cells that are thinner in radial section and broader in tangential section. Bisporangia measure 15–70 µm broad and 55–120 µm long. Conceptacles become embedded in the perithallus. Algae are violet reddish in color.

Habitat and Comments: *Hyperandri bisporum* grows on mangrove roots, other coralline algae, and gastropods (*Lobatus gigas*). The species has been collected from the intertidal to 70 m depth, commonly together with *Magnephycus ornatus*. [Additional illustrations: Athanasiadis and Ballantine 2024: figs. 37–41; as *Phymatolithon bisporum*, Afonso-Carrillo 1984: figs. 15–16, 19, 20.]

FIGURE 20. *Hyperandri bisporum*. AAPR-27B, herbarium specimen with multiporate bisporangial conceptacles growing on *Lobatus gigas* shell, La Parguera, 1.0 m. Scale bar = 500 µm.

Magnephycus Athanas. et D.L.Ballant.

Magnephycus Athanas. et D.L.Ballant. 2024: 130.

Thalli are saxicolous, epizoic, or epiphytic on the roots of *Rhizophora mangle*, strongly or moderately adhering to the substratum. The encrusting base secondarily forms a foliose habit with unattached-superposed growth. Thallus organization is dorsiventral with a polystromatic, non-coaxial hypothallus (coaxial regions occur in certain species) supporting a gradually ascending perithallus lacking protuberances. The perithallus is non-stratified and of limited growth, lacking embedded conceptacles. Subepithallial cells are longer than cells below, supporting a single rectangular, generally flattened epithallial cell. Cell fusions are common. Secondary pit connections and trichocytes are absent. Gametophytes are dioecious, and the conceptacles are conical. Spermatangial conceptacles develop simple (rarely dendroid) spermatangial structures on the floor, the walls, and the roof. In the generitype, spermatangia develop on a pedestal formed by up to 7 or 8 layers of isodiametric cells borne on a layer of palisade cells (Athanasiadis and Ballantine 2024: fig. 5n–q). Carposporangial conceptacles lack a pedestal and develop carposporangia from the periphery. Multiporate conceptacles are hemispherical (wartlike) and develop pyriform canals. Filaments lining the canals are composed of 5 cells, those near the surface being similar to neighboring roof cells, whereas basal and subbasal cells are thinner in radial section and broader in tangential section, stain darker, and project outward (hence the pyriform canal shape). Older conceptacles senesce and do not become embedded in the perithallus. The generitype of the three recognized *Magnephycus* species (Athanasiadis and Ballantine 2024) occurs in Puerto Rico.

Magnephycus ornatus (Foslie et M.Howe) Athanas. et D.L.Ballant.

FIGURE 21

Magnephycus ornatus (Foslie et M.Howe) Athanas. et D.L.Ballant. 2024: 131, figs. 51–55.

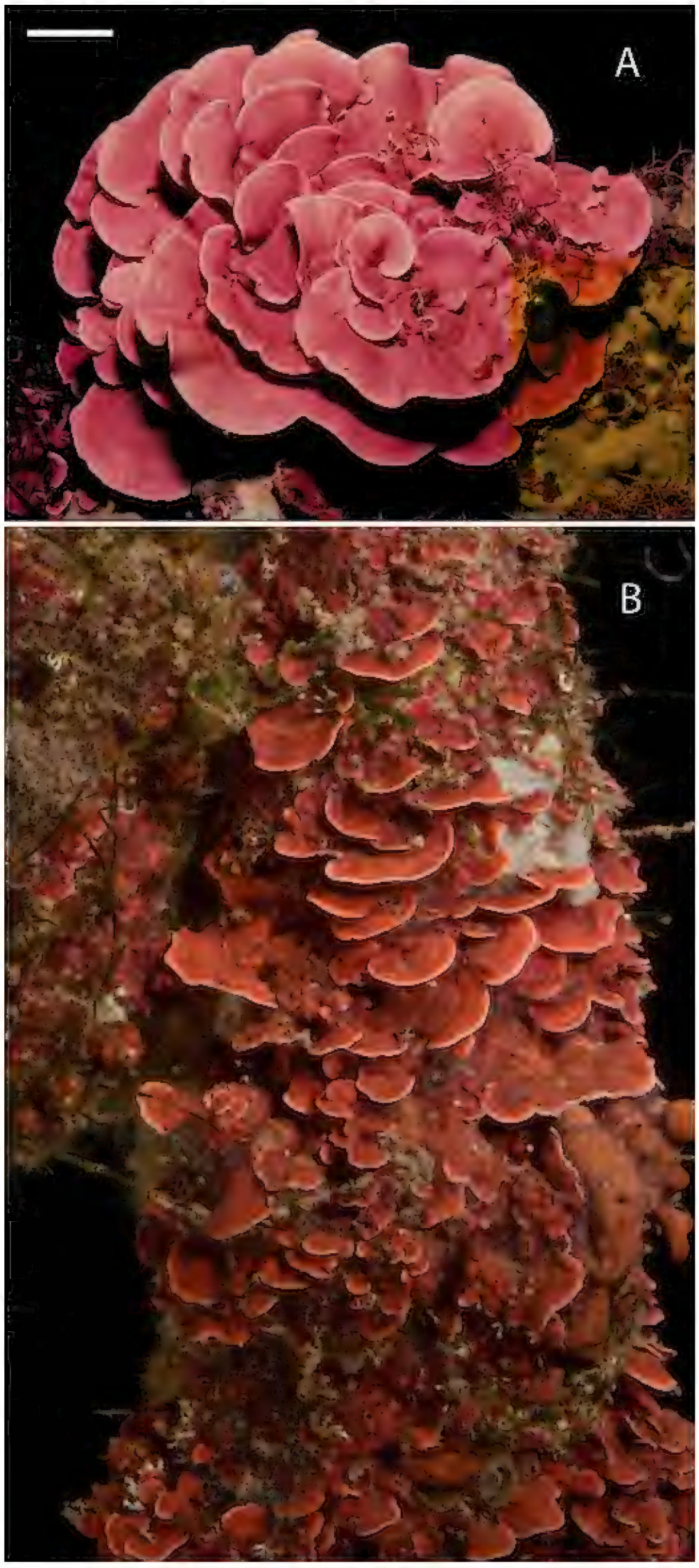

FIGURE 21. *Magnephycus ornatus*. (A) DLBsn, habit of live specimen grown in saltwater tank, Magueyes Island, La Parguera. Scale bar = 0.5 cm. (B) In situ photograph, growing on *Rhizophora mangle* prop roots, Collado Reef, La Parguera, 17 m. Field is approximately 10 cm.

Basionym: Lithothamnion mesomorphum var. *ornatum* Foslie et M.Howe 1906a: 129, pl. 80: fig. 2, pl. 90: fig. 2.

Homotypic Synonyms: Mesophyllum mesomorphum var. *ornatum* (Foslie et M.Howe) M.J.Wynne 1998: 110; *Mesophyllum ornatum* (Foslie et M.Howe) Athanas. 1999a: 246–247.

Puerto Rican Records: As *Mesophyllum ornatum*: Ballantine et al. 2011. As *Magnephycus ornatus*: Athanasiadis and Ballantine 2024.

Western Atlantic Distribution: Costa Rica, Bahamas, Bermuda, Barbados, Puerto Rico, U.S. Virgin Islands, Colombia.

Type Locality: Cave Cays, Exuma Chain, Bahamas.

Thalli develop foliose complexes to 8.0 cm in extent, composed of a basal encrusting layer supporting unattached-superimposed lamellae with lobate margins. Individual lamellae are 60–380 µm thick, composed of a non-coaxial hypothallus with limited perithallial development. Cells of the hypothallus are 3.0–11 µm broad and 6.0–38 µm long. Perithallial cells are 4.0–8.0 µm broad and 4.0–16 µm long. Cell fusions are present, and secondary pit connections and trichocytes are lacking. Gametophytes are dioecious, and the conceptacles are conical. Carposporangial conceptacles are 500–860 µm diam. and 310–525 µm high. Male conceptacles measure 330–750 µm diam. and 180–330 µm high. Spermatangia develop on a pedestal, extending along the entire fertile floor and forming up to 7–8 layers of isodiametric cells where the basal layer is usually composed of palisade cells. Hemispherical tetrasporangial conceptacles are wartlike and measure 440–680 µm diam. and 200–310 µm high. Tetrasporangia are 15–65 µm diam. and 110–150 µm long. Algae are yellowish pink to rose red in color.

Habitat and Comments: *Magnephycus ornatus* is a common alga in shady and sheltered littoral sites in crevices attached to rock and corals as well as epiphytically on prop roots of *Rhizophora mangle*. Puerto Rican specimens have been collected from the shallow littoral to 70 m depths. The species is easily distinguished from two other foliose corallines that occur in Puerto Rico, *Neogoniolithon solubile* and *Mesophyllum mesomorphum*, by the absence of a coaxial hypothallus and the presence of lobate margins in the thallus. [Additional illustrations: Athanasiadis and Ballantine 2024: figs. 51–55; as *Lithothamnion mesomorphum* var. *ornatum*, Foslie and Howe 1906a: 129, pl. 80: fig. 2, pl. 90: fig. 2.]

Melyvonneeae Athanas. et D.L.Ballant.

Melyvonnea Athanas. et D.L.Ballant.

Melyvonnea Athanas. et D.L.Ballant. 2014: 391.

Thalli grow either as attached crusts with erect protuberances or as unattached subspherical rhodoliths. They possess a multilayered hypothallus that is predominantly coaxial. The perithallus is also multilayered and stratified, composed of elongate subepithallial cells and flattened epithallial cells. Erect perithallial protuberances are secondarily formed and may

become branched, gradually dominating the encrusting base. Trichocytes occur terminally among epithallial cells. Cell fusions between vegetative cells are common, and secondary pit connections are absent. Gametophytes are monoecious, with females producing moderately projecting conceptacles. Carposporangial chambers are spheroid in shape, lacking a central pedestal. Tetrasporangial conceptacles develop sunken canals with a wider base, and pore filaments lining the canals possess elongate basal cells. Older conceptacles become embedded in the perithallus. *Melyvonnea* is a tropical and subtropical genus, represented in Puerto Rico by two (of the four known) species (Athanasiadis and Ballantine 2014, 2024).

KEY TO *MELYVONNEA* SPECIES OF PUERTO RICO

1. Thalli are free-living (rhodoliths) with up to 7 erect perithallial protuberances per square cm; 5-celled filaments line canals of multiporate conceptacles . . . . . ***M. aemulans***
   Thalli are free-living or attached with up to 27 erect perithallial protuberances per square cm; 3–4-celled filaments line canals of multiporate conceptacles . . . . . ***M. erubescens***

Melyvonnea aemulans (Foslie et M.Howe) Athanas. et D.L.Ballant.

Melyvonnea aemulans (Foslie et M.Howe) Athanas. et D.L.Ballant. 2014: 394, figs. 3–18.

Basionym: *Lithothamnion fruticulosum* var. *aemulans* Foslie et M.Howe 1906a: 130, pl. 81: figs. 1, 2.

Homotypic Synonyms: *Lithothamnion aemulans* (Fosle et M.Howe) Foslie 1908c: 17; Foslie 1908d: 9–10; *Mesophyllum aemulans* (Foslie et M.Howe) W. H. Adey 1970: 22.

Puerto Rican Records: Athanasiadis and Ballantine 2014, 2024. As *Lithothamnion fruticulosum* var. *aemulans*: Foslie and Howe 1906a. As *Lithothamnium aemulans*: Foslie 1908d; Taylor 1960; Ballantine and Aponte 1997a. As *Mesophyllum aemulans*: Ballantine and Aponte 2002a.

Western Atlantic Distribution: Puerto Rico.

Type Locality: San Juan, Puerto Rico.

Thalli are free-living nodules to 10 cm in extent and 150–1400 µm thick, with up to 7 (per square cm) erect perithallial protuberances, 2.0–5.0 mm long and 1.5–5.0 mm broad. The coaxial hypothallus is 50–150 µm thick, composed of cells 5.0–10 µm broad and 12–22 µm long. The ascending perithallus is 40–500 µm thick, composed of cells 4.0–12 µm broad and 5.0–24 µm long that show stratification. Subepithallus meristematic cells are elongate, to 13 µm in length, each supporting a single, flattened, epithallial cell, 5.0–12 µm diam. and 1.5–3.0 µm long. Carpogonial conceptacles measure 50 µm diam. and 150 µm high, with a chamber 245 µm in diam. and 70 µm high. Multiporate conceptacles are 385–500 µm diam. and to 90 µm high, with a convex to flattened roof. Canals are 6.0–8.0 µm diam. and barely visible in surface view, lined by 5-celled filaments, having elongate basal cells and isodiametric upper cells. The roof is 35–48 µm thick, composed of 5–6 cells. Embedded chambers are 212–370 µm diam. and 120–165 µm high, filled in with palisade cells. Older conceptacles become overgrown by peripheral filaments, forming protuberances, 450–700 µm diam. and 90–180 µm high. Tetrasporangial remains are 75–140 µm long and 40–70 µm broad.

Habitat and Comments: Despite the multiple records, a comparative study of the original and later material deposited in NY and MSM showed that *Melyvonnea aemulans* is known only from the type collection in shallow water at San Juan (Athanasiadis and Ballantine 2014: 394–399). The original material (Howe no. 2237) was a single specimen encircling a coral. During the preparation of the protologue (Foslie and Howe 1906a: pl. 81: figs. 1, 2), this specimen was divided into two pieces, with one fragment (holotype) deposited in the Foslie herbarium in TRH (Adey and Lebednik 1967) and the other (isotype) deposited in NY. [Illustrations: as *Melyvonnea aemulans*, Athanasiadis and Ballantine 2014: figs. 3–18; as *Lithothamnion aemulans*, Printz 1929: pl. 12: fig. 21; as *Lithothamnion fruticulosum* var. *aemulans*, Foslie and Howe 1906a: 130, pl. 81: figs. 1, 2.]

Melyvonnea erubescens (Foslie) Athanas. et D.L.Ballant.

FIGURE 22

Melyvonnea erubescens (Foslie) Athanas. et D.L.Ballant. 2014: 405, figs. 62–106.

Basionym: Lithothamnium erubescens Foslie 1900a: 9.

Puerto Rican Records: Athanasiadis and Ballantine 2014, 2024.

Western Atlantic Distribution: United States (Louisiana, Texas), Bermuda, Bahamas, Cuba, Puerto Rico, Brazil.

World Distribution: See Athanasiadis and Ballantine 2024.

Type Locality: Chaloup Bay, Fernando de Noronha, Brazil.

Thalli form a crustose basal portion, 100–1,100 µm thick, that gives rise to erect, up to 27 (36) perithallial protuberances per square cm. Individuals reach up to at least 18 cm in extent and up to 5 cm high. The erect protuberances are to 15(–30) mm high and 1.0–4.0(–5.0) mm thick and may demonstrate anastomoses. The coaxial hypothallus is 45–180 µm thick, composed of cells 2.0–10 µm broad and 8.0–32 µm long. The ascending perithallus measures 20–900 µm thick, with cells 3.0–10 µm broad and 3.0–20 µm long and shows stratification. Terminal trichocytes, 10–13 µm broad and 13–20 µm long, occur on perithallial filaments and on conceptacle roofs. Subepithallial meristematic cells are elongate, 4.5–15.0 µm long, each supporting a single flattened, epithallial cell, 4–10 µm

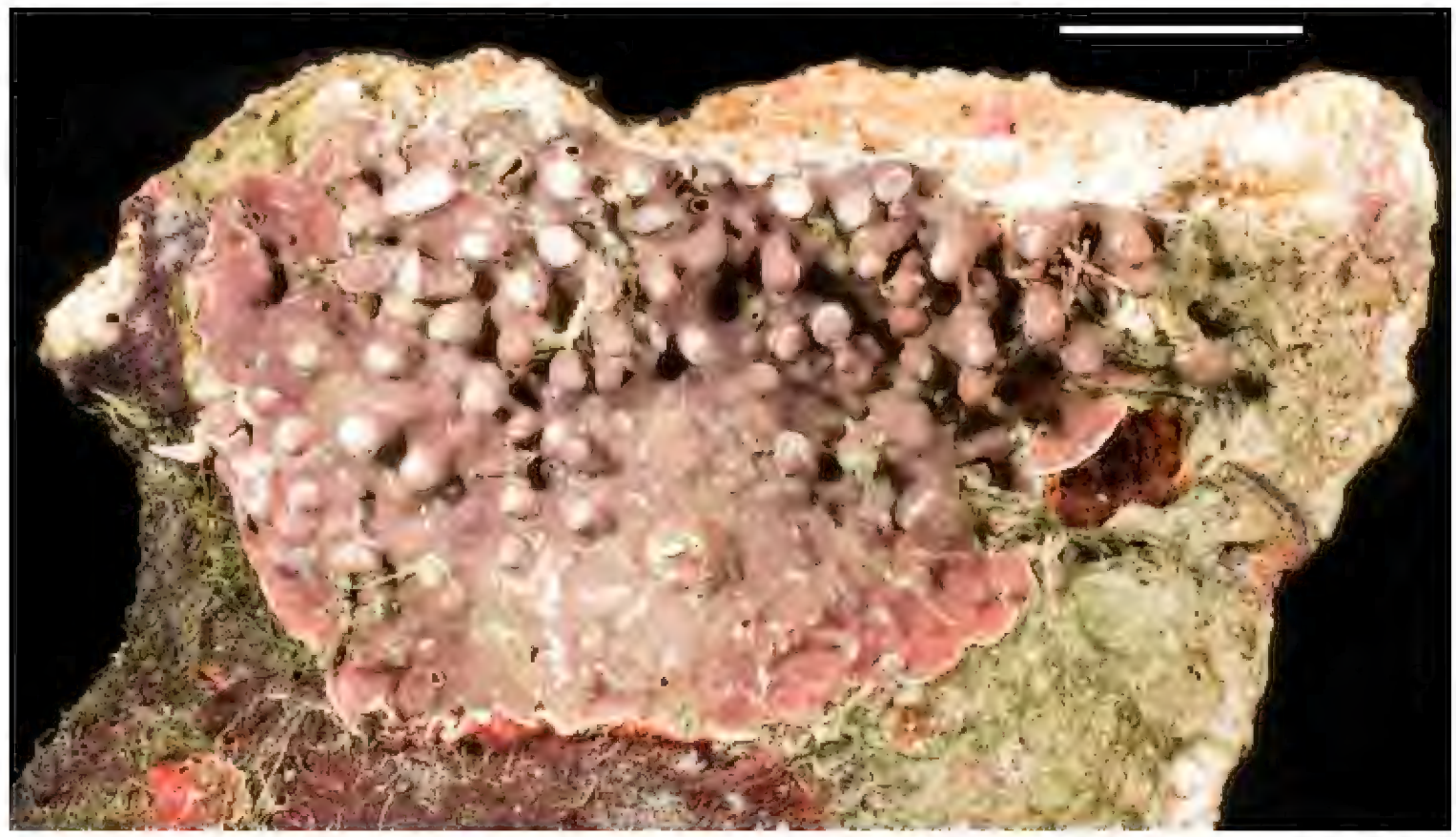

FIGURE 22. *Melyvonnea erubescens*. AAPR-115 (in GB), herbarium specimen, Media Luna Reef, off La Parguera, 0.5–1.0 m. Scale bar = 2.0 cm.

diam. and 1.0–2.5 µm long. Cell fusions are common, whereas secondary pit connections are absent. Gametophytes are monoecious. Male conceptacles measure 240–550 µm diam. and are up to 240 µm high. Carposporangial conceptacles measure 550–1,200 µm diam. and are 150–390 µm high, with carposporangia 50–70 µm diam. Conceptacles may develop in superimposition, and older conceptacles become embedded in the perithallus. Multiporate tetrasporangial conceptacles measure 220–580 µm diam. and 70–180 µm high. Filaments lining the canals are 3–4-celled, having elongate (15–17 µm long) basal cells that are thinner in radial section and broader in tangential section, with characteristically shorter subepithallial cells than normal roof cells. Zonately divided tetrasporangia are 30–90 µm diam. and 80–160 µm long, and the bisporangia are 30–80 µm diam. and 90–120 µm long.

Habitat and Comments: Specimens of *Melyvonnea erubescens* from Puerto Rico have been collected in shallow water to a depth of 2.0 m, attached to *Rhizophora mangle* roots in sheltered environments, on stones in tide pools, and in protected crevices on corals and sponges at exposed sites. Duplicates are deposited in GB, TRH, and MSM (see Athanasiadis and Ballantine 2014: 409). A Howe (no. 2196) bi/tetrasporangial collection from a tide pool in Santurce is annotated by Foslie as "*Lithoth. syntrophicum* forma?" (TRH, B16 2524; Athanasiadis and Ballantine 2014: 409, 432). Specimens forming rhodolith beds at depths down to 25 m are reported from Brazil (Horta et al. 2011; Sissini et al. 2014; Jesionek et al. 2016). [Additional illustrations: Athanasiadis and Ballantine 2014: figs. 62–106; Jesionek et al. 2016: fig. 9; Amado-Filho et al. 2018: figs. 2C, 3D; as *Mesophyllum erubescens*, Sissini et al. 2014: figs. 7–10.]

Mesophyllum Me.Lemoine

Mesophyllum Me.Lemoine 1928: 252.

Thalli are saxicolous, epizoic, or epiphytic, strongly or moderately adhering to the substratum. At least two species are known to form rhodoliths. The encrusting thallus either secondarily forms a foliose habit with unattached-superimposed growth or produces erect perithallial protuberances that remain unbranched. Thallus organization is dorsiventral, with a polystromatic, predominantly coaxial hypothallus supporting a gradually ascending perithallus. The perithallus is stratified or not with limited or extensive growth, in the latter case supporting embedded conceptacles. Subepithallial cells are longer than cells below, supporting a single rectangular (generally flattened) or rounded epithallial cell. Cell fusions are common. Secondary pit connections and trichocytes are absent. All conceptacles project moderately and develop oblong chambers. Gametophytes are dioecious. Spermatangial conceptacles develop simple spermatangia on all surfaces of the conceptacle chamber. Carposporangial conceptacles form a pedestal on the fertile floor via partial dissolution of the surrounding cells. Carposporangia develop from the periphery of the fusion cell and bend down to fill the empty space of the chamber. Multiporate conceptacles develop a convex, flattened, or concave roof (in the latter case provided with a rim or not). Pore canals are straight. Filaments lining the canals are composed of more than 5 cells that are similar in length, stain darker, and/or are thinner in radial section and broader in tangential section. Older conceptacles senesce or become embedded in the perithallus.

Mesophyllum is a predominantly cold temperate genus, well represented on the Pacific coast of North America between the Aleutians and the deep sublittoral of Baja California. Two of the 12 recognized species (Athanasiadis and Ballantine 2024) occur in Puerto Rico.

KEY TO *MESOPHYLLUM* SPECIES OF PUERTO RICO

1. Thalli moderately attached, foliose with unattached superimposed growth . . . . . ***M. mesomorphum***
   Thalli firmly attached with limited unattached growth. . . . . ***M. syntrophicum***

Mesophyllum mesomorphum (Foslie) W.H.Adey

Mesophyllum mesomorphum (Foslie) W.H.Adey 1970: 25.
Basionym: Lithothamnion mesomorphum Foslie 1901: 5.
Puerto Rican Records: Athanasiadis and Ballantine 2014, 2024.
Western Atlantic Distribution: Bermuda, Hispaniola, Old Providence Island, Puerto Rico, Colombia.
World Distribution: See Athanasiadis and Ballantine 2014, 2024.
Type Locality: Bermuda.

Thalli have an encrusting base, secondarily producing foliose, lamellate, imbricate complexes, irregularly lobed and proliferating, reaching 5.0–6.0(–13) cm in extent and 300–500(–1,500) µm thick. The proliferations are semicircular or irregular and loosely spreading over each other. Individual lamellae are up to 850 µm thick and are composed of a predominantly coaxial hypothallus, 30–350 µm thick, producing an ascending stratified perithallus to 500 µm thick. Hypothallus cells are (2.0–)5.0–8.0(–10) µm broad and (8–)12–20(–31) µm long. Perithallial cells are 1.5–8.0 µm broad and 5–12 µm long. Epithallial cells are flattened, 5.0–8.0 µm in diam. and 1.5–3.0 µm long. Cell fusions between contiguous vegetative cells are common. Secondary pit connections and trichocytes are absent. Gametophytes are unknown. Tetrasporangial conceptacles are subprominent, 600–700 µm diam. and 110–120 µm high, with a convex roof, and usually are coalescing. Tetrasporangia measure 30–55 µm diam. and 100–220 µm long. Older conceptacles become embedded in the perithallus. Algae are red in color.

Habitat and Comments: *Mesophyllum mesomorphum* is not common in Puerto Rico, being known from only a sublittoral collection at Las Creras, Aguadilla. The species could be confused with *Magnephycus ornatus*, which lacks a coaxial hypothallus, or *Neogoniolithon solubile*, which exhibits a coaxial hypothallus, but differs in developing trichocytes, uniporate tetrasporangial conceptacles with elongate canals, and a limited perithallus. [Illustrations: Littler and Littler 2000: 35; Athanasiadis and Ballantine 2014: figs. 109–130.]

Mesophyllum syntrophicum (Foslie) W.H.Adey

FIGURE 23
Mesophyllum syntrophicum (Foslie) W.H.Adey 1970: 26.
Basionym: *Lithothamnion syntrophicum* Foslie 1901: 6.
Puerto Rican Records: Athanasiadis and Ballantine 2014, 2024.
Western Atlantic Distribution: Bermuda, Jamaica, Puerto Rico.
Type Locality: Harrington Sound, Bermuda.

Thalli are predominantly encrusting and strongly adhering, with rare unattached margins, at least 4.3 cm in extent and several mm thick via superimposition. Individual lamellae are 75–850 µm thick, composed of a predominantly coaxial hypothallus, 30–180 m thick, supporting an ascending stratified perithallus, to 600 m thick. Hypothallial cells are 3.0–9.0 µm broad and 10–30 µm long, and perithallial cells measure 4.0–8.0 µm broad and 4.0–15 m long. Epithallial cells, borne singly on elongate subepithallial meristematic cells, are flattened, 5.0–9.0 µm diam. and 1.5–3.0 µm long. Cell fusions between vegetative cells are common. Secondary pit connections or trichocytes are absent. Gametophytes are unknown. Multiporate conceptacles measure 330–850 µm diam. and 50–280 µm high, and the roof is flattened or convex. Tetrasporangia are 55–95 µm diam. and 90–185 µm long. Bisporangia measure 45–70 µm diam. and 75–145 µm long. Older conceptacles become embedded in the perithallus.

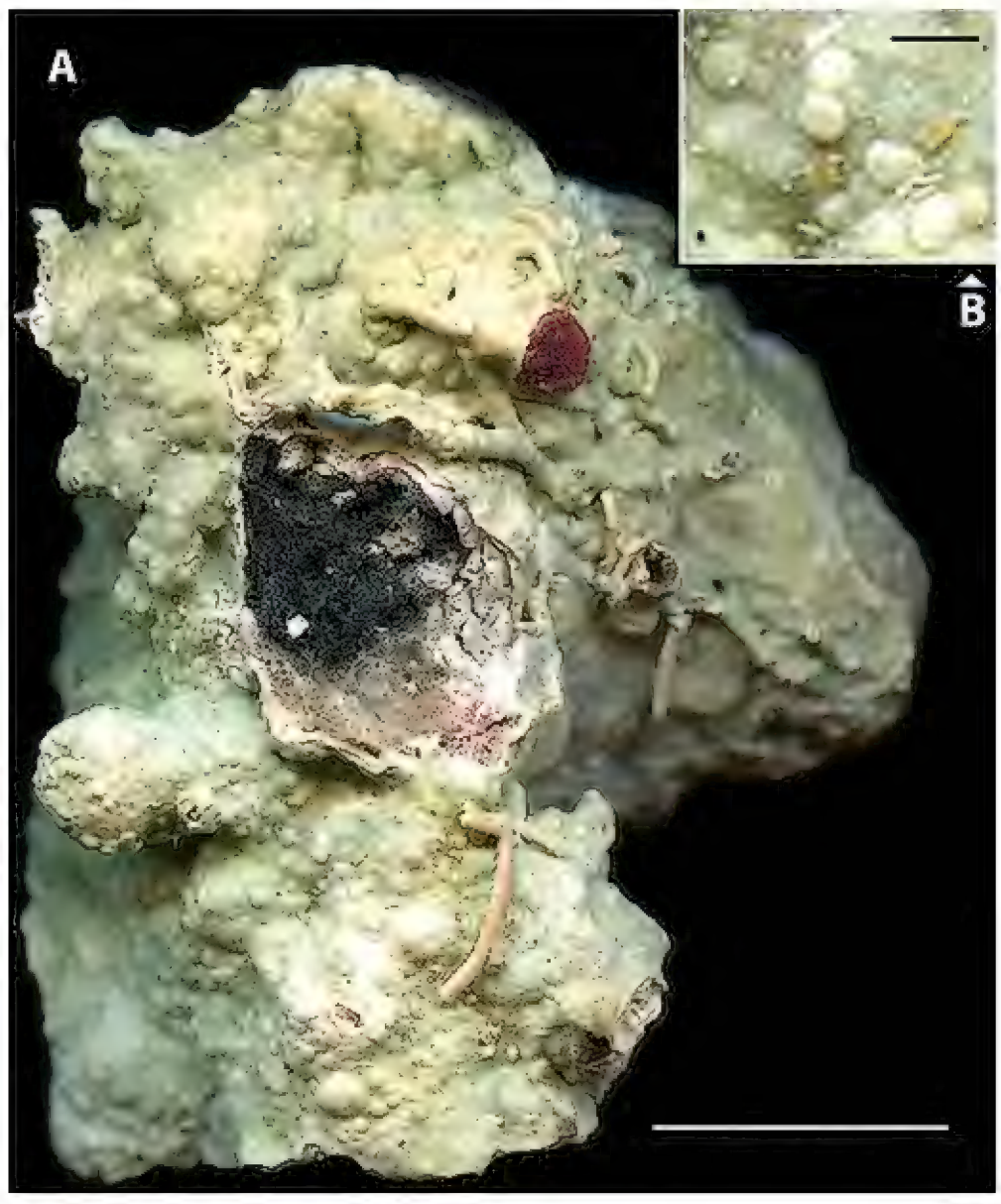

FIGURE 23. *Mesophyllum syntrophicum*. AAPR-133 (in GB). (A) Herbarium specimen, growing on corals and rocks, with *Melyvonnea erubescens*, Media Luna Reef, off La Parguera, 0.5–1.0 m. Scale bar = 1.0 cm. (B) Convex conceptacles on the thallus surface. Scale bar = 1 mm.

Habitat and Comments: Type specimens are described as "lying loose at the bottom" (Foslie 1901: 6). Herbarium specimens are attached to polychaete tubes, stones, and other hard substrata, usually in association with the foraminifera *Miniacina miniacea* (Pallas). A Puerto Rican specimen was collected in a crevice at an exposed site, attached to a coral with other encrusting algae in the upper sublittoral zone (0.5–1 m depth). A Bermudan record, reported from 54 m depth (Frederick 1963: 65, as *Lithothamnion syntrophicum*) has not been reexamined. Specimens collected by Howe (as *Lithothamnion syntrophicum*) from Santurce and deposited in the Foslie herbarium (Adey and Lebednik 1967) represent misidentifications (see Athanasiadis and Ballantine 2014: 432). [Additional illustrations: Athanasiadis and Ballantine 2014: figs. 133–145.]

Spongitidaceae Kütz.[3]

Hydrolithoideae A. Kato et Baba in Kato et al.

Fosliella M.Howe

Fosliella M.Howe 1920b: 587

[3] Contributed by A. Athanasiadis, D. L. Ballantine, J. N. Norris, and H. Ruiz.

Thalli are typically epiphytic on algae and marine angiosperms, occasionally epilithic or epizoic. Thallus organization is heterotrichous ("dimerous" sensu Woelkerling 1988: 7, 227), composed of a monostromatic hypothallus of rectangular (non-palisade) cells, producing a limited perithallus (usually absent or up to 12 cells thick), with terminal rounded **epithallial** cells. Cell fusions are common between vegetative cells, and secondary pit connections are absent. Trichocytes are produced terminally on hypothallial cells and may also occur on perithallial filaments around conceptacles. Propagules are sometimes present. Hypothallial filaments are occasionally unconsolidated (as seen in *Fosliella farinosa* var. *chalicodictya*). Gametophytes are usually monoecious. Carposporangial conceptacles possess an elongate canal. Tetra/bisporangial conceptacles are uniporate, with pore canals lined by cells oriented perpendicularly to the roof surface. Reproductive characters are similar to *Hydrolithon*. A spore germination disk develops a central element of 4 cells (as in *Hydrolithon*). *Fosliella* occurs in tropical and temperate parts of the world, with some 25 species described (see Index Nominum Algarum, 2024), 5 of which are currently accepted taxonomically (Guiry and Guiry 2024), and 2 of which, including the generitype, *F. farinosa*, are recorded in Puerto Rico.

KEY TO THE *FOSLIELLA* SPECIES OF PUERTO RICO

1. Thalli typically 1–3 cells thick ..... *F. farinosa*
   Thalli usually more than 5 cells thick ..... *F. chamaedoris*

Fosliella chamaedoris (Foslie et M.Howe) M.Howe

FIGURE 24

Fosliella chamaedoris (Foslie et M.Howe) M.Howe 1920b: 588.

Basionym: *Lithophyllum chamaedoris* Foslie et M.Howe 1906a: 134, pl. 90: fig. 1.

Homotypic Synonyms: Melobesia chamaedoris (Foslie et M.Howe) Foslie 1908a: 6; *Heteroderma chamaedoris* (Foslie et M.Howe) Foslie 1909: 57; *Hydrolithon chamaedoris* (Foslie et M.Howe) M.J.Wynne 2005: 12, 81.

Puerto Rican Records: As *Hydrolithon chamaedoris*: Ballantine et al. 2011.

Western Atlantic Distribution: Bahamas, Puerto Rico, U.S. Virgin Islands.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Exuma Chain, Cave Cays, Bahamas.

Thalli form small crusts 60–150 µm thick, composed of a monostromatic hypothallus with cells 6.0–13 µm diam. and 11–25 µm long (seen from the surface). The perithallus forms up to 12 layers and is up to 150 µm thick. Vertically elongate perithallial cells measure 7.0–11 µm diam. and 10–12 µm long, seldom 14 µm long. "Two-parted" sporangia (Foslie and Howe 1906a: 134) measure 30–40 µm diam. and 50–60 µm long. Algae are dull rose or purplish in color.

Habitat and Comments: According to Foslie (1908a: 6–7, 1908d: 17–18), the protologue of *Lithophyllum chamaedoris* Foslie et M.Howe (1906a) describes carposporangial conceptacles with "two-parted" sporangia representing gonimoblasts, whereas apparently both Taylor (1960: 389) and Littler and Littler (2000: 24) interpreted this to be the presence of bisporangia in the species, which is incorrect. Puerto Rican thalli measure to 6 cells and ~75 µm in thickness, forming crusts completely encircling the annulated stipes of *Chamaedoris peniculum* (J.Ellis et Sol.) Kuntze (Ballantine et al. 2023). *Fosliella chamaedoris* is not a commonly reported species, previously known only from the Bahamas (Howe 1920b) and the U.S. Virgin Islands (Lemoine in Børgesen, 1917, as *Melobesia chamaedoris*). The species is probably more common in the Caribbean than indicated by the few records. [Additional illustration: Littler and Littler 2000: 25.]

Fosliella farinosa (J.V.Lamour.) M.Howe

FIGURE 25A

Fosliella farinosa (J.V.Lamour.) M.Howe 1920b: 587.

Basionym: Melobesia farinosa J.V.Lamour. 1816: 315, pl. XII: fig. 3.

Homotypic Synonym: Hydrolithon farinosum (J.V Lamour.) Penrose et Y.M.Chamb. 1993: 295.

Puerto Rican Records: As *Melobesia farinosa*: Hauck 1888. As *Fosliella farinosa*: Taylor 1960; Almodóvar 1965; Ballantine 1979, 1984; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Costa Rica, Panama, Caribbean Mexico, United States (Florida, North Carolina), Bahamas, Barbados, British Honduras, Cuba, Guadeloupe, Hispaniola, Jamaica, Old Providence, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Epiphytic on *Fucus linifolius* Turner [=*Sargassum acinarium* (L.) Setch.], Mediterranean Sea.

Thalli form fragile and lightly calcified crusts, from 2.0 to 5.0 mm or more in extent and ~20 µm thick. The hypothallus is single layered and forms fanlike concentric arrangements. Hypothallial cells measure 12–20(–30) µm long and 7.0–10(–18) µm broad. Colorless trichocytes, 22–40 µm long and 15–18 µm broad, bear hairs and occur terminally on hypothallial or short perithallial filaments (the latter surrounding conceptacles). Conceptacles are uniporate. Sporangial and cystocarpic conceptacles measure 140–250 µm diam., and spermatangial conceptacles are smaller. Zonately divided tetrasporangia measure (20–)30–50 µm diam. and (40–)50–90 µm long. Tetrasporangia measure (20–)30–50 µm diam. and (40–)50–90 µm long. Algae are pinkish or white in color.

Habitat and Comments: *Fosliella farinosa* commonly grows as an epiphyte on larger algae as well as on hard substrata. The species occurs in both shallow and deepwater habitats. Specimens collected by Howe from Culebra, Guánica, and Aguadilla are deposited in the Foslie herbarium (Adey and Lebednik 1967, as *Melobesia farinosa*). [Additional illustrations: as *Hydrolithon farinosum*, Penrose and Chamberlain 1993: figs. 1–19; Mendoza-González et al. 2009: fig. 3; Won et al. 2010: figs. 18–24; Cormaci et al. 2017: FP211, figs. 6, 7.]

FIGURE 24. *Fosliella chamaedoris*. DLB6498, live specimen, seaward Punta Brea algal plain, 17 m, epiphytic on *Chamaedoris peniculum*. Scale bar = 2.0 cm.

Fosliella farinosa var. *chalicodictya* W.R.Taylor

FIGURE 25B

Fosliella farinosa var. *chalicodictya* W.R.Taylor 1939: 10–12, figs. 13, 14, pl. 1: figs. 1–3.
Homotypic Synonym: Hydrolithon farinosum var. *chalicodictyum* (W.R.Taylor) Serio 1994: 969.
Puerto Rican Records: Ballantine et al. 2016b.
Western Atlantic Distribution: Bermuda, Puerto Rico, Colombia.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Old Providence Island, Colombia.

Thalli are small, delicate, and lightly calcified crusts reaching 1.0–2.0 mm in extent. Hypothallial filaments, 10–12 µm diam., are unconsolidated and sinuous. The central portions of cells adhere where making contact, resulting in a crust with a netlike appearance. Hypothallial cells are 10–12 µm diam. and 15–20 µm long, with small superficial epithallial cells and occasional trichocytes, 18–22 µm diam., terminating filaments.

Habitat and Comments: In Puerto Rico *F. farinosa* var. *chalicodictya* has an epiphytic habit and has only rarely been collected in deeper water, to 61 m (Ballantine et al. 2016b). The variety was originally collected on *Valonia ventricosa* J.Agardh (Taylor 1939) and differs from the nominate species by nature of its netlike appearance of unconsolidated hypothallial filaments. [Additional illustrations: as *Fosliella farinosum* var. *chalicodictya*, Taylor 1939: 10–12, figs. 13, 14, pl. 1: figs. 1–3; as *Hydrolithon farinosum* var. *chalicodictyum*, Schneider and Searles 1997: figs. 1–3.]

Hydrolithon (Foslie) Foslie

Hydrolithon (Foslie) Foslie 1909: 55.
Basionym: Goniolithon subgenus *Hydrolithon* Foslie 1905b: 7.

Thalli are encrusting, attached to hard substrata, usually rock, or sometimes occur as unattached rhodoliths. The thallus surface is smooth, reflecting the substratum underneath, or develops extensive perithallial protuberances that dominate over the basal crust. The thallus organization is heterotrichous ("dimerous" sensu Woelkerling 1988: 7, 227), composed of a

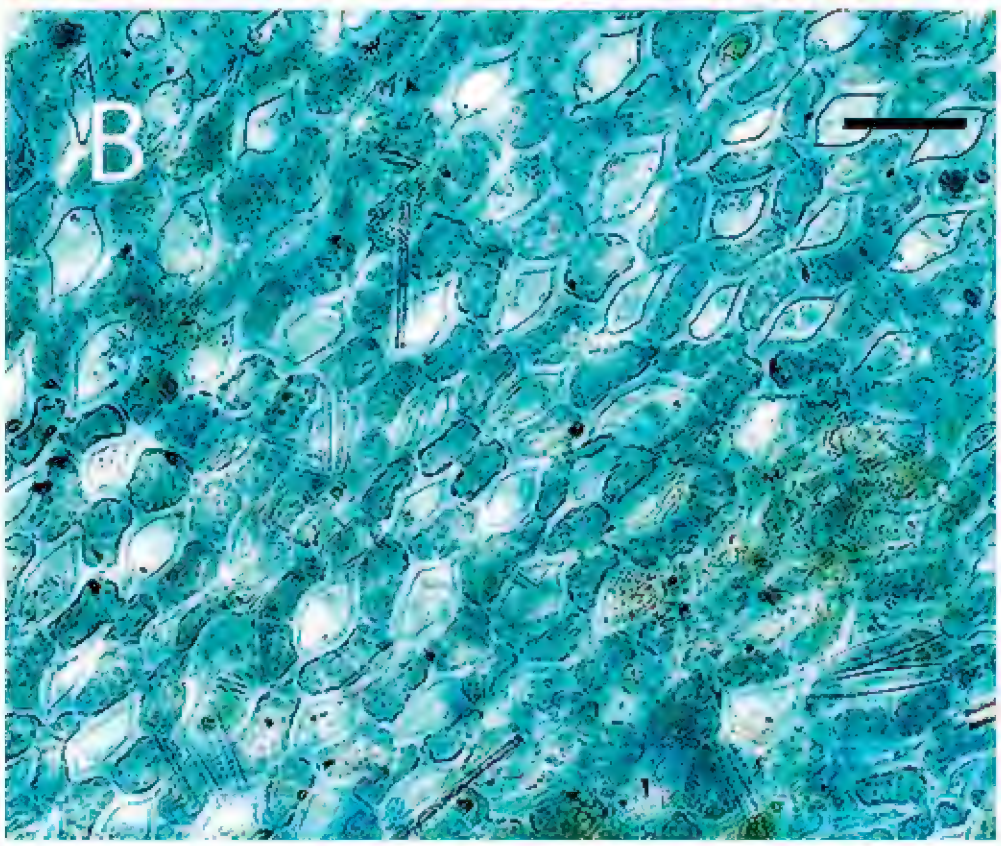

FIGURE 25. *Fosliella farinosa*. (A) In situ habit photograph, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Epiphytic on *Udotea flabellum*. Field width = approximately 15 cm. (B) *Fosliella farinosa* var. *chalicodictya*. DLB1711, shelf edge seaward La Parguera, 58 m depth, growing on sponge *Verongia*. Micrograph illustrating netlike growth. Scale bar = 25 µm.

monostromatic hypothallus supporting an erect polystromatic perithallus. Hypothallial and perithallial cells are irregularly shaped, and the latter terminate in trichocytes or epithallial cells. Trichocytes occur singly, in pairs, or in horizontal/vertical series (groups) and may become embedded in the perithallus. Epithallial cells occur singly, rarely 2 or 3 (4), and are flattened or rounded. Intercellular fusions occur between contiguous vegetative cells, and secondary pit connections are absent. Spermatangial conceptacles develop simple spermatangia on the floor, and carposporangial conceptacles produce carposporangia from the periphery of the fusion cell. Tetra/bisporangial conceptacles produce a sunken ostiole, and the canal is lined by pore cells oriented perpendicularly to the roof surface (see Penrose and Woelkerling 1992: figs. 4, 5). The generitype *H. reinboldii* (Weber Bosse et Foslie) Foslie is based on a collection from Moearas Reef, East Borneo (East Kalimantan), Indonesia, and remains poorly known. Two of the 22 currently recognized species of *Hydrolithon* occur in Puerto Rico.

KEY TO THE *HYDROLITHON* SPECIES OF PUERTO RICO

1. Thalli lacking erect protuberances and encrusting hard substrata in the sublittoral, to at least 70 m depth . . . ***H. abyssophila***
   Thalli with conspicuous perithallial protuberances, growing on hard substrata in the lower littoral . . . . . ***H. antillarum***

***Hydrolithon abyssophila* Athanas., D.L.Ballant. et H.Ruiz**

FIGURE 26

Hydrolithon abyssophila Athanas., D.L.Ballant. et H.Ruiz 2013: 496, figs. 1–17.

Puerto Rican Records: Athanasiadis et al. 2013; Ballantine et al. 2016b; Sherman et al. 2023.

Western Atlantic Distribution: Puerto Rico, U.S. Virgin Islands.

Type Locality: Insular shelf edge, "Hole in the wall," off La Parguera, Puerto Rico.

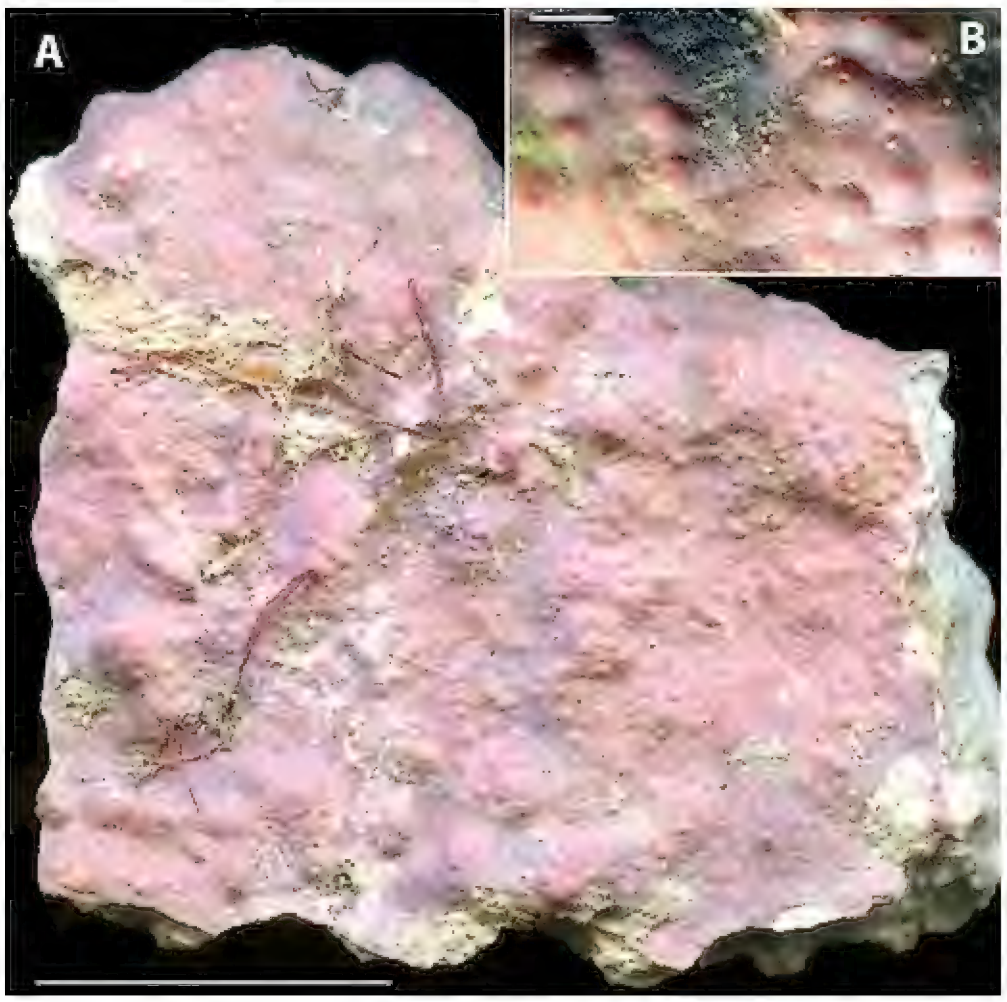

FIGURE 26. *Hydrolithon abyssophila*. (A) Live specimen with uniporate conceptacles and *Gelidium "calcicola-penetrans"* nom. ined. on its thallus. "Hole in the wall," edge of insular shelf, 50 m. Scale bar = 1.0 cm. (B) Detail of conceptacles. Scale bar = 500 µm.

Thalli are encrusting, at least 10 cm in extent. The thallus surface usually displays shallow, craterlike depressions and irregular projections that reflect the substratum underneath. Perithallial protuberances are lacking. Hypothallial cells are variously shaped (usually rectangular to trapezoid) and measure 10–28 µm long and 5.0–10(–35) µm broad. Perithallial cells are 7.0–18 µm long and 5.0–15 µm broad. Flattened epithallial cells, 6.0–10 µm diam. and 1.0–2.0 µm long, are borne singly. Terminal trichocytes, 28–32 µm long and 10–18 µm broad, occur rarely and are solitary among epithallial cells. Uniporate, bisporangial conceptacles are crowded, generally projecting above the thallus surface and occurring in patches. Individual conceptacles measure 270–475 µm in external diameter and 20 to 175 µm high. Gametangial thalli are apparently dioecious (only carpogonial conceptacles have been observed). Carpogonial conceptacles are uniporate, occurring across the thallus surface, and measure 415–460 µm in external diameter and 75–120 µm high. Algae are pink in color.

Habitat and Comments: *Hydrolithon abyssophila*, described from an insular shelf habitat on the south coast of Puerto Rico, is an obligate deepwater species known from 30 m to at least 76 m depths. The species is extremely abundant and is probably to be found at mesophotic depths throughout the Caribbean and, perhaps by cover, is the most common benthic eukaryotic organism in the Caribbean at depths greater than 50 m (Ballantine and Ruiz, unpublished). Sherman et al. (2023) reported that the dominant coralline algae in Puerto Rican shelf edge cores from 49 to 57 m was *Hydrolithon abyssophila*.

***Hydrolithon antillarum* (Foslie et M.Howe) Athanas. et D.L.Ballant. comb. nov.**

FIGURE 27

Hydrolithon antillarum (Foslie et M.Howe) Athanas. et D.L.Ballant. comb. nov.

Basionym: Lithophyllum antillarum Foslie et M.Howe 1906b: 579, text fig. 2, pls. 25, 26.

Homotypic Synonym: Porolithon antillarum (Foslie et M.Howe) Foslie et M.Howe in Foslie 1909: 57.

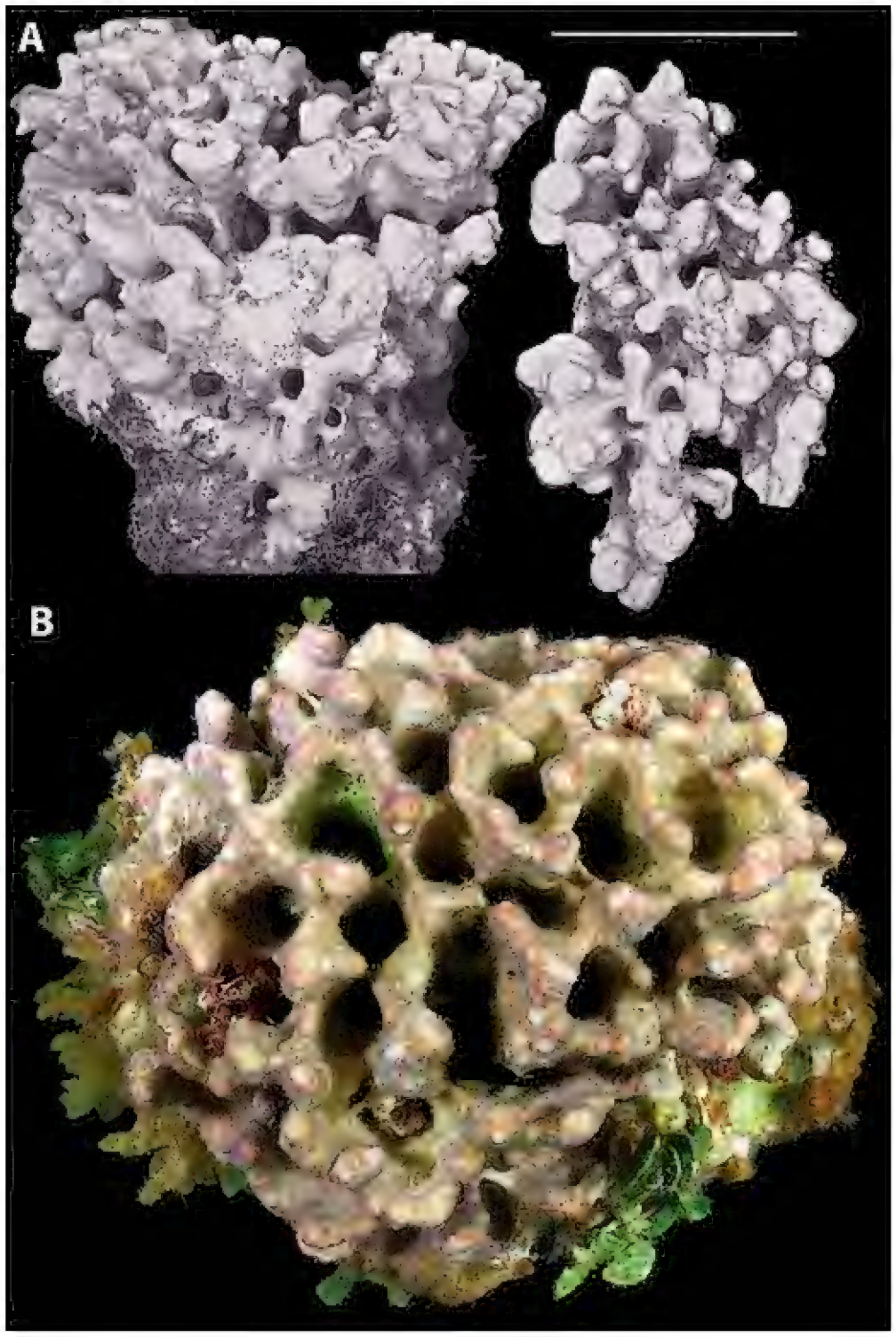

FIGURE 27. *Hydrolithon antillarum*. (A) Type specimens from Culebra Island in NY. Scale bar = 5 cm. Reproduced from Foslie and Howe (1906a: pl. 25) with modifications. (B) DLB8357, live specimen from Cocos Beach, Mona Island, 1.0–3.0 m. Scale bar = 1.0 cm.

Puerto Rican Records: As *Lithophyllum antillarum*: Foslie and Howe 1906b; Printz 1929. As *Porolithon antillarum*: Foslie 1909; Gabrielson et al. 2018 (conspecific with *Porolithon pachydermum*).
Western Atlantic Distribution: Puerto Rico.
Type Locality: Flamingo Bay, Culebra Island, Puerto Rico.

Thalli saxicolous or epizoic (on corals), forming erect protuberances, somewhat columnar rather flat-topped masses 10–30 cm high and 8.0–20 cm broad. The protuberances form an almost solid, confluent mass at the base, becoming lacunate and anastomosing toward the apices. The free portions mostly 5.0–25 mm broad and 3.0–12 mm thick, often enlarging upward. The perithallus comprises subquadrate or roundish cells, 7.0–10 µm diam., becoming elongate in the erect branches, 7.0–18 × 7–10 µm. Trichocytes are clustered, occurring in horizontal groups among the uppermost perithallial cells as well as deeper in the thallus. They measure 20–33 µm long and 14–20 µm diam. Tetrasporangial conceptacles are uniporate, 150–300 µm diam., and project slightly (Foslie et Howe 1906b: text fig. 2a). They become embedded in the perithallus. Tetrasporangia measure 20–40 µm diam. and 38–70 µm long. Thalli are grayish pink or pale in color.

Habitat and Comments: *Hydrolithon antillarum* has been characterized as "evidently a reef-builder" (Foslie and Howe 1906b: 579), but there are few accounts of its structure and reproduction. The original material was growing at the low-water mark on a coral reef. Foslie and Howe (1906b: pl. 25, lower specimen) selected a (holo)type (about 10 × 10 cm in extent), presently deposited in NY, whereas other specimens of the original collection (Howe no. 4373) are deposited in TRH, BM, NY, and PC (Printz 1929: pl. 68: figs. 5, 6; Woelkerling 1993: 28; Maneveldt and Keats 2014: 230). The second plate in the protologue (Foslie and Howe 1906b: pl. 26), said to show a "medullary hypothallium," illustrates embedded "rows of enlarged cells" (trichocytes), indicating that the tissue engulfing the trichocytes is a perithallus that shows apparent stratification, as shown by Maneveldt and Keats (2014: fig. 28) in a type specimen (TRH 27–1565).

Maneveldt and Keats (2014: figs. 27–29, 30, 32, 38) further demonstrated the presence of (1) up to 4 epithallial cells, (2) trichocytes in horizontal groups, (3) enlarged pore cells located at the base of the canal of a tetrasporangial conceptacle, and (4) a monostromatic basal layer (hypothallus) supporting erect (perithallial) filaments (the hypothallial cells being pit connected to the proximal perithallial cells). These features, which also occur in the generitype of *Hydrolithon*, *H. reinboldii* (Weber Bosse et Foslie) Foslie (see Penrose and Woelkerling 1988: figs. 2, 7, 8, 1992: fig. 3), support the transfer of *Lithophyllum antillarum* to *Hydrolithon*. A proposal to treat *Porolithon pachydermum* as a molecular synonym of *H. antillarum* (Gabrielson et al. 2018) is not accepted and is discussed under the account of *P. pachydermum*.

The original material of *H. antillarum* is deposited in NY (holotype), TRH (Printz 1929: pl. 68: figs. 5, 6, as *Lithophyllum*), and also PC and BM (Maneveldt and Keats 2014, as *Porolithon*). [Additional illustrations: as *Lithophyllum antillarum*, Printz 1929: pl. 68: figs. 5, 6; as *Porolithon antillarum*, Maneveldt and Keats 2014: figs. 25–38.]

Pneophyllum Kütz.

Pneophyllum Kütz. 1843: 385.

Thalli are lightly calcified epilithic or epiphytic crusts, measuring less than 200 µm in extent and up to 2–3(–5) cells thick. Thalli are composed of a single-layered hypothallus of rectangular (non-palisade) cells that produces either a single layer of epithallial cells or erect perithallial filaments at right angles (ending in a layer of epithallial cells). Cell fusions between vegetative cells are common, and secondary pit connections are absent.

Trichocytes (when present) develop in an intercalary position within hypothallial filaments or laterally, replacing perithallial or epithallial cells. Tetra/bisporangial conceptacles are uniporate, and the pore cells protrude laterally in the canal (Rosanoff 1866: fig. 8, as *Melobesia lejolisii*; Chamberlain 1983: figs. 14, 16). Reproductive characters are similar to *Hydrolithon* and *Fosliella*. A spore germination disk develops a central element of 8 cells. The genus occurs in all parts of the world except the polar regions. Twenty *Pneophyllum* species are currently recognized, of which one, the generitype, is recorded in Puerto Rico.

Pneophyllum fragile Kütz.

Pneophyllum fragile Kütz. 1843: 385.

Heterotypic Synonyms: *Melobesia lejolisii* Rosanoff 1866: 62, pl. 1: figs. 1–13; *Fosliella lejolisii* (Rosanoff) M.Howe 1920b: 588; *Pneophyllum lejolisii* (Rosanoff) Y.M.Chamb. 1983: 359, figs. 28–32.

Puerto Rican Records: As *Pneophyllum fragile*: Ballantine and Aponte 1997a, 2002a. As *Melobesia lejolisii*: Almodóvar and Blomquist 1959. As *Fosliella lejolisii*: Almodóvar and Ballantine 1983; Hinds and Ballantine 1987.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida, Texas), Bermuda, Bahamas, Barbados, Belize, Cuba, French Guiana, Hispaniola, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Epiphytic on *Sphaerococcus coronopifolius* L., Mediterranean Sea (Chamberlain 1983: 353, fig. 24).

Thalli are delicate crusts, 0.5–2.0 mm diam., composed of 2–4 cell layers, 15–30 µm thick, with a single-cell-thick margin. Square to rectangular hypothallial cells, 5.0–10 µm diam. and 5.0–20 µm long, are radially oriented and dichotomously branched in concentric arrangements. Trichocytes, when present, develop in an intercalary position in hypothallial filaments and are 8.0–13 µm diam. The perithallus has 1–3 layers and bears single epithallial cells, 6.0–12 µm wide and 3.0–12 µm long. Conceptacles are either flush with the thallus surface or slightly raised, 150–250(–300) µm diam. Tetrasporangia measure 50–80 µm long and 30–50 µm diam. Algae are pink in color.

Habitat and Comments: Thalli growing on the seagrass *Zostera marina* L. were previously segregated as *Pneophyllum lejolisii* from *P. fragile* that inhabits larger algae (Chamberlain 1983). These two taxa are still considered to be two distinct forms of a single species by Chamberlain (1994: 143). *Pneophyllum fragile* is a common epiphytic species in Puerto Rico. [Illustrations: as *Pneophyllum fragile*, Schneider and Seales 1991; Littler et al. 2008: 28; as *Pneophyllum lejolisii*, Littler and Littler 2000: 39; as *Melobesia lejolisii*: Suneson 1937: figs. 1–5.]

Neogoniolithoideae A.Kato et Baba in Kato et al.

Neogoniolithon Setch. et L.R.Mason

Neogoniolithon Setch. et L.R.Mason 1943: 92.

Thalli are heavily calcified, encrusting or leafy forms, profusely branched, whose bases can be closely adherent to the substrata. Some species form rhodoliths. The thallus surface is smooth or provided with extensive perithallial protuberances that dominate over the crustose base. The hypothallus is polystromatic, coaxial in the generitype, and arches upward to support a multitiered perithallus. Perithallial filaments may bear single, terminal or intercalary trichocytes sometimes in horizontal or vertical series. Epithallial cells are rounded or rectangular but not flared. Adjacent cells of vegetative filaments may fuse but lack secondary pit connections. Gametophytes are dioecious. Conceptacles are prominently elevated over the thallus surface and usually provided with an elongate canal. Pore cells protrude laterally in the canal of tetra/bisporangial conceptacles. In contrast to other members of the family, tetrasporangia are relatively small (shorter than the chamber height), spermatangia develop on all surfaces within the conceptacle chamber, and carposporangia are borne across the dorsal side of the fusion cell. Forty-three species of *Neogoniolithon* are recognized worldwide, six of which occur in Puerto Rico. One of them, *N. solubile*, is considered to be a putative synonym of the generitype, *N. fosliei* (Heydr.) Stech. et L.R.Mason, from the Red Sea.

KEY TO THE *NEOGONIOLITHON* SPECIES OF PUERTO RICO

1. Thalli with erect perithallial protuberances 2
   Thalli lacking perithallial protuberances 4
2. Protuberances distinctively compressed at their apex . . . . . *N. acropetum*
   Protuberances distinctively terete at their apex 3
3. Thalli unattached; trichocytes occurring in vertical series . . . . . *N. spectabile*
   Thalli attached or unattached; trichocytes occurring singly . . . . . *N. strictum*
4. Hypothallus coaxial . . . . . *N. solubile*
   Hypothallus non-coaxial 5
5. Thalli forming thin crusts, rarely superposed . . . . . *N. accretum*
   Thalli forming squamulose-imbricate crusts . . . . . *N. propinquum* f. *imbicillum*

Neogoniolithon accretum (Foslie et M.Howe) Setch. et L.R.Mason

FIGURE 28

Neogoniolithon accretum (Foslie et M.Howe) Setch. et L.R.Mason 1943: 90.

Basionym: Goniolithon accretum Foslie et M.Howe 1906a: 131, pl. 85: fig. 2, pl. 91.

Homotypic Synonym: Lithophyllum accretum (Foslie et M Howe) Me.Lemoine in Børgesen 1917: 159.

Puerto Rican Records: As *Neogoniolithon accretum*: Ballantine and Aponte 1997a, 2002a; Ballantine et al. 2005; Ruiz and Ballantine 2009. As *Goniolithon accretum*: Taylor 1960.

Western Atlantic Distribution: United States (Florida, North Carolina), Bahamas, Jamaica, Puerto Rico.

World Distribution: Japan.

Type Locality: Sands Key, Florida.

Thalli form thin crusts closely adhering to pebbles or rock, following the irregularities of the substratum underneath and lacking perithallial protuberances. Individual lamellae are 80–340 µm thick, rarely reaching 1.3 mm (via superposition). Hypothallial cells are 8.0–14 µm broad and 14–27 µm long. Perithallial cells are subquadrate or roundish, 4.0–9.0 µm diam., sometimes either elongated, to 10 µm, or becoming wider. Trichocytes are 20–25 µm long. Conceptacles (of unknown content) are about 300–400 µm diam. Algae are light rose to slightly yellowish in color.

Habitat and Comments: *Neogoniolithon accretum* has been reported to be a common, although easily overlooked, member of the coral reef algal flora at shelf edge reefs on the south coast of Puerto Rico. A disease, coralline white band syndrome, was reported by Ballantine et al. (2005) and affected more than 70% of the algal colonies at the edge of insular shelf off La Parguera. The disease condition results in killing all algal tissue affected and is easily recognizable by a distinctive white band at the front of the pathogen spread.

The protologue (cited above) describes thalli growing on exposed surf-beaten rocks, or pebbles in more protected places, and a single specimen (~3.5 × 7.5 cm) from Sands Key (Florida) was illustrated and selected as the (holo)type from Howe's collection no. 2920a (Foslie and Howe 1906a: pl. 85: fig. 2). A second specimen from Howe's original collection is deposited in TRH (Printz 1929: pl. 45: fig. 20; Adey and Lebednik 1967; Woelkerling et al. 2005). Five other Howe collections were cited, including two from Puerto Rico (Foslie and Howe 1906a: 131), but the original account ends with the remark "specimens seen are mostly sterile and the species is perhaps not a well-defined one." Lemoine (in Børgesen 1917: 159, as *L. accretum*) described Børgesen's material from St. Croix and also studied Howe's material from the Bahamas, but her account is in variance with the protologue, as it includes data for a coaxial hypothallus, suggesting the presence of different taxa in the collections. Setchell and Mason (1943: 90–91) separated *N. accretum* from *N. affine*, placing the former within the group "Crustaceae" and the latter within "Verrucosae aut ramosae." Masaki (1968: 46, pls. 33, 34, 73–75) reported the species from Japan, pointing out that his material was in good agreement with the protologue but not Lemoine's account. Masaki also recorded carposporangia on "the whole surface of the floor" and spermatangia on "the whole inner surface of conceptacles," which in combination with the uniporate conceptacles and the multilayered hypothallus are diagnostic features of the genus *Neogoniolithon*.

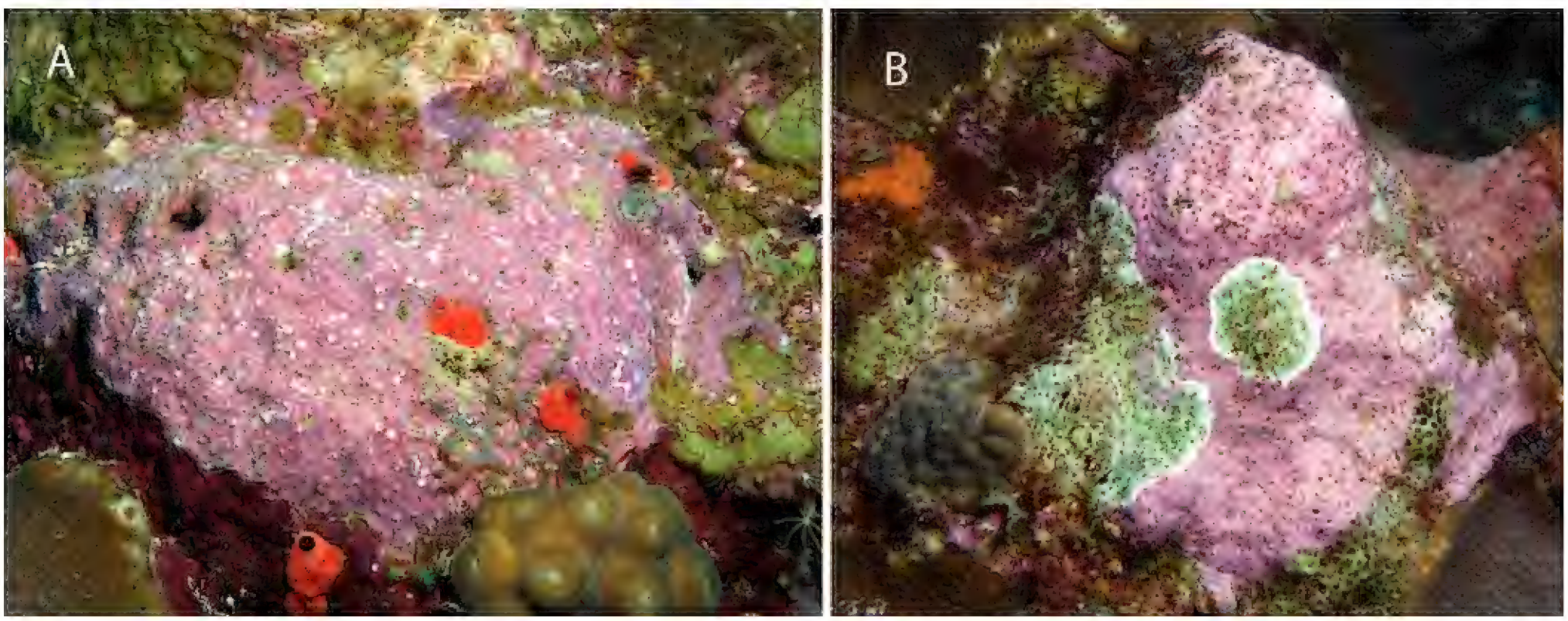

FIGURE 28. *Neogoniolithon accretum*. (A) In situ habit photograph from edge of insular shelf, offshore from La Parguera, 18 m. Field is approximately 10 cm. (B) In situ habit photograph from edge of insular shelf, offshore from La Parguera, 18 m. Colony showing coralline white band syndrome, a disease condition. Field is approximately 10 cm.

Mateo-Cid et al. (2014: 71, figs. 2–9) described dioecious gametophytes and tetrasporophytes from Mexico and confirmed the generic position of the species. They noted, however, a maximum thallus thickness of up to 800 µm versus 1,300 µm in the holotype—the latter resulted via superposition. Foslie and Howe (1906a: pl. 91) commented that "in no other specimen . . . we observed superposed layers."

Richards et al. (2021: 1236) located the holotype in NY and proposed synonymy with *Spongitis (Harveylithon) munita*, using partial sequences but without comparing the diagnostic morpho-anatomical characters of these two species. However, the fruticose thallus of the lectotype and all syntypes of *Spongitis (Lithophyllum) munita* (Printz 1929: pl. 54: figs. 16, 17; Richards et al. 2021: fig. 4) contrast markedly with the smooth surface of the holotype, paratypes, and all other reported specimens of *Neogoniolithon accretum* (Foslie and Howe 1906a: 131, pl. 85: fig. 2; Printz 1929: pl. 45: figs. 19, 20; Masaki 1968: pl. 33; Mateo-Cid et al. 2014: fig. 2). We therefore consider that the synonymy proposed by Richards et al. merits confirmation, pending comparison of new material from the type localities of these two species.

Specimens collected by Howe from San Juan and Guánica are deposited in the Foslie herbarium (Adey and Lebednik 1967: 24, as *Goniolithon accretum*). [Additional illustrations: as *Neogoniolithon accretum*, Masaki 1968: pls. 33, 34, 73–75; Mateo-Cid et al. 2014: figs. 2–9; as *Goniolithon accretum*, Foslie and Howe 1906a: pl. 85: fig. 2, pl. 91; Printz 1929: pl. 45: figs. 19, 20.]

Neogoniolithon acropetum (Foslie et M.Howe) W.H.Adey

Neogoniolithon acropetum (Foslie et M.Howe) W.H.Adey 1970: 8.

Basionym: *Goniolithon acropetum* Foslie et M.Howe 1906b: 577, text fig. 1, pls. 23, 24.

Puerto Rican Records: As *Goniolithon acropetum*: Printz 1929; Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, Bahamas, Puerto Rico.

Type Locality: Culebra Island, Puerto Rico.

Thalli form irregular masses, measuring 4.0–12 cm high and 6.0–15 cm diam. Individuals may become confluent, resulting in larger colonies. Polymorphic branches are produced from a rather inconspicuous hypothallus. Branches are repeatedly subdichotomous, anastomosing, compressed or subterete, 1.3–3.10 mm diam., and have flabellate, compressed tips at least 2.0 mm diam. Perithallial cells measure 9.0–14 µm diam. and 11–21 µm long. Trichocytes are abundant. Tetrasporangial conceptacles are subconical to mammilliform, measuring to 1.0 mm diam. Tetrasporangia measure 40–102 µm diam. and 90–168 µm long. Algae are grayish pink in color when living.

Habitat and Comments: *Neogoniolithon acropetum* has only rarely been collected since the type collection in a shallow, sheltered environment at Culebra Island at about 0.1–0.4 m depth (low tide) attached to corals and other encrusting corallines. According to the protologue (cited above), specimens are fertile (tetrasporophytic) at the beginning of March. The top specimen illustrated in plate 23 of Foslie and Howe (1906b) was selected as the (holo)type, and other specimens with the same Howe collection number (no. 4224) were deposited in NY, BM, and TRH (Printz 1929: pl. 51: figs. 2–5; Woelkerling 1993; Woelkerling et al. 2005). The report of "medullary" hypothallial cells in the protologue (Foslie and Howe 1906b: pl. 24), said to be 14–40 × 11–20 µm, pertains to perithallial cells since it was most likely based on the relevant illustration, which shows a section of a branch (perithallus) and not the basal layer (hypothallus).

Mateo-Cid et al. (2014) found only tetrasporophytes at several localities in Mexico and also described the trichocytes (30–35 × 45–50 µm) to be scattered or in vertical series. [Illustrations: as *Goniolithon acropetum*, Foslie and Howe 1906b: pls. 23, 24; Printz 1929: pl. 51: figs. 2–5; as *Neogoniolithon acropetum*, Mateo–Cid et al. 2014: figs. 10–14.]

Neogoniolithon propinquum (Foslie) Me.Lemoine f. *imbicillum* (Foslie) Me.Lemoine

Neogoniolithon propinquum f. *imbicillum* (Foslie) Me.Lemoine 1966: 12.

Basionym: Goniolithon propinquum f. *imbicillum* Foslie 1908b: 4 (as "*imbicilla*").

Puerto Rican Records: Foslie 1908b; Printz 1929.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Santurce, Puerto Rico.

Thalli strongly attached, encrusting, squamulose-imbricate, with conical to convex tetrasporangial conceptacles measuring (300–)350–500 µm diam. Perithallial cells possess numerous fusions between adjacent cells and lack secondary pit connections. The hypothallus consists of several layers, 12–22 µm wide and 20–32 µm long. Trichocytes are somewhat smaller than in the autonym, where they attain a size of 22–36 µm broad and 25–64 µm long.

Comments: In the protologue (cited above), Foslie described *Neogoniolithon propinquum* f. *imbicillum* as a "forkrøblet" (deformed) growth of the species corresponding to *Goniolithon notarisii* f. *ptychoides* Foslie (type locality: Tangiers, Morocco). The latter entity is a well-known reef builder in Tunisia, Mediterranean Sea (Denizot et al. 1981: 253–66). Unfortunately, later information on f. *imbicillum* is lacking. The size of tetrasporangial conceptacles (said to be 400–500 µm in the diagnosis but (300)350–500 µm in the main text) suggests that f. *imbicillum* should rather be referred to *N. accretum* or possibly recognized as an independent species (with emphasis on its imbricate thallus). In transferring f. *imbicillum* to *Neogoniolithon*, Lemoine (1966: 12, fig. E) described

conceptacles fitting the size of the autonym (*N. propinquum*) but gave no information about f. *imbicillum*. Two Howe collections from Puerto Rico are deposited in TRH with duplicates in NY (Adey and Lebednik 1967: 27; Woelkerling et al. 2005: 93). These include the TRH lectotype from Santurce, San Juan, selected by Woelkerling (1993: 120) and previously illustrated by Printz (1929: pl. 45: fig. 15), and a collection from Culebra Island (not listed in the protologue). [Illustration: Printz 1929: pl. 45: fig. 15.]

Neogoniolithon solubile (Foslie et M.Howe) Setch. et L.R.Mason

FIGURE 29

Neogoniolithon solubile (Foslie et M.Howe) Setch. et L.R.Mason 1943: 90.

Basionym: Goniolithon solubile Foslie et M.Howe in Foslie 1907b: 21.

Homotypic Synonyms: Goniolithon propinquum f. *solubile* (Foslie et M.Howe) Foslie 1908b: 4; *Paragoniolithon solubile* (Foslie et M.Howe) W.H.Adey, R.A.Towns. et Boykins 1982: 12.

Puerto Rican Records: As *Goniolithon solubile*: Foslie 1907b; Taylor 1960; Woelkerling et al. 2005. As *Neogoniolithon solubile*: Ballantine and Aponte 2002a; Mateo-Cid and Pedroche 2004. As *Paragoniolithon solubile*: Woelkerling 1987.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Bahamas, Barbados, Cuba, Hispaniola, Jamaica, Puerto Rico, U.S. Virgin Islands, St. Bartholomew, Brazil, Colombia.

Lectotype Locality: Culebra Island, Puerto Rico, fide Adey 1970

Thalli are primarily adherent, becoming irregularly shaped leafy crusts, 0.2–0.8 mm thick and to 5 cm in extent, often superposed and enclosing small coral fragments. Individuals can be strongly or loosely adherent, forming 2–3 layers on top of each other. Their surface is uneven, somewhat rugged with concentric proliferations. The hypothallus dominates (1/2 to 3/4) the thallus thickness and is composed of filaments with coaxial growth and rectangular cells, 11–24 µm diam. and 25–46 µm long. The perithallus is weakly developed, composed of cells 10–14 µm diam. and 11–18 µm long. Lateral fusions occur between adjacent vegetative cells, and secondary pit connections are absent. Trichocytes are present in small numbers. Tetrasporangial conceptacles are conical and apiculate with an elongate canal, 0.6–1.0 mm diam. Tetrasporangia measure 30–40 µm diam. and 70–80 µm long. Algae are purple in color.

Habitat and Comments: Our account describes the habit of the species as given in the protologue, which is based on thalli from Culebra Island growing attached to *Porolithon pachydermum* and overgrowing other smaller substrata. A second specimen from Jamaica cited in the protologue was found to differ with respect to the hypothallus (Adey 1970: 9), and its identity was questioned, rendering Culebra Island as the lectotype locality. Howe (1920b: 585) reported that Bahamian specimens occurred on "old corals, coral pebbles, and old shells in shallow water, sometimes covering and smothering living corals of fruticose habit." Tetrasporangial thalli have also been collected in shallow water at Gustavia Bay (St. Bartholomew), growing unattached (DLB3441). Mateo-Cid et al. (2014) reported both male gametophytes and tetrasporophytes on the Atlantic coast of Mexico.

Neogoniolithon solubile is a common sublittoral alga in Puerto Rico resembling *Mesophyllum mesomorphum* in habit. Both species develop a coaxial hypothallium but can be distinguished by the diminutive perithallus and the presence of trichocytes in *N. solubile*. Moreover, tetrasporangial conceptacles are convex and multiporate in species of *Mesophyllum*, whereas they are conical and uniporate with elongate canals in species of *Neogoniolithon*.

Mateo-Cid and Pedroche (2004: table 1) proposed synonymy between *N. solubile* and the generitype *N. fosliei* from the Red Sea after showing that their types possess a similar thallus structure and reproduction, including the size of vegetative cells, trichocytes, tetrasporangia, and tetrasporangial conceptacles. Woelkerling (1987: 147), who also compared the relevant types, considered them to be "probable conspecific." *Neogoniolithon fosliei* is widely reported in the Indo-Pacific (see Adey et al. 1982), whereas *N. solubile* is recorded only from the western Atlantic. The genetic diversity between Caribbean and Indo-Pacific populations awaits to be studied before conspecificity should be accepted.

The lectotype specimen collected by Howe from Culebra and illustrated by Printz (1929) is deposited in the Foslie herbarium in TRH (Adey and Lebednik 1967, as *Goniolithon solubile*). [Additional illustrations: as *Goniolithon solubile*, Printz 1929: pl. 45: fig. 14; Taylor 1960: pl. 76: fig. 3; as *Neogoniolithon solubile*, Mateo-Cid and Pedroche 2004: pl. 1: figs. 1, 2; pl. 2: figs. 7, 8; Mateo-Cid et al. 2014: figs. 61–69; as *Paragoniolithon solubile*, Woelkerling 1987: figs. 1, 3, 4.]

Neogoniolithon spectabile (Foslie) Setch. et L.R.Mason

Neogoniolithon spectabile (Foslie) Setch. et L.R.Mason 1943: 92.

Basionym: *Goniolithon spectabile* Foslie 1901: 16–18.

Puerto Rican Records: As *Goniolithon spectabile*: Printz 1929; Taylor 1960. As *Neogoniolithon spectabile*: Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, Bermuda, United States (Florida), Bahamas, Belize, Hispaniola, Puerto Rico, Turks and Caicos, Netherlands Antilles, Colombia.

Type Locality: Bermuda.

Heavily calcified rhodoliths occur in subspherical growths, reaching 32 cm long and 24 cm broad (in the lectotype) but reported as smaller, to 12 cm in extent, by Taylor (1960). Thalli are irregularly and abundantly subdichotomously and irregularly branched. The terete or subterete branches possess slightly elevated protuberances that taper from the base, 1.5–3.0(–5.0) mm diam., with the terminal divisions being hardly more than

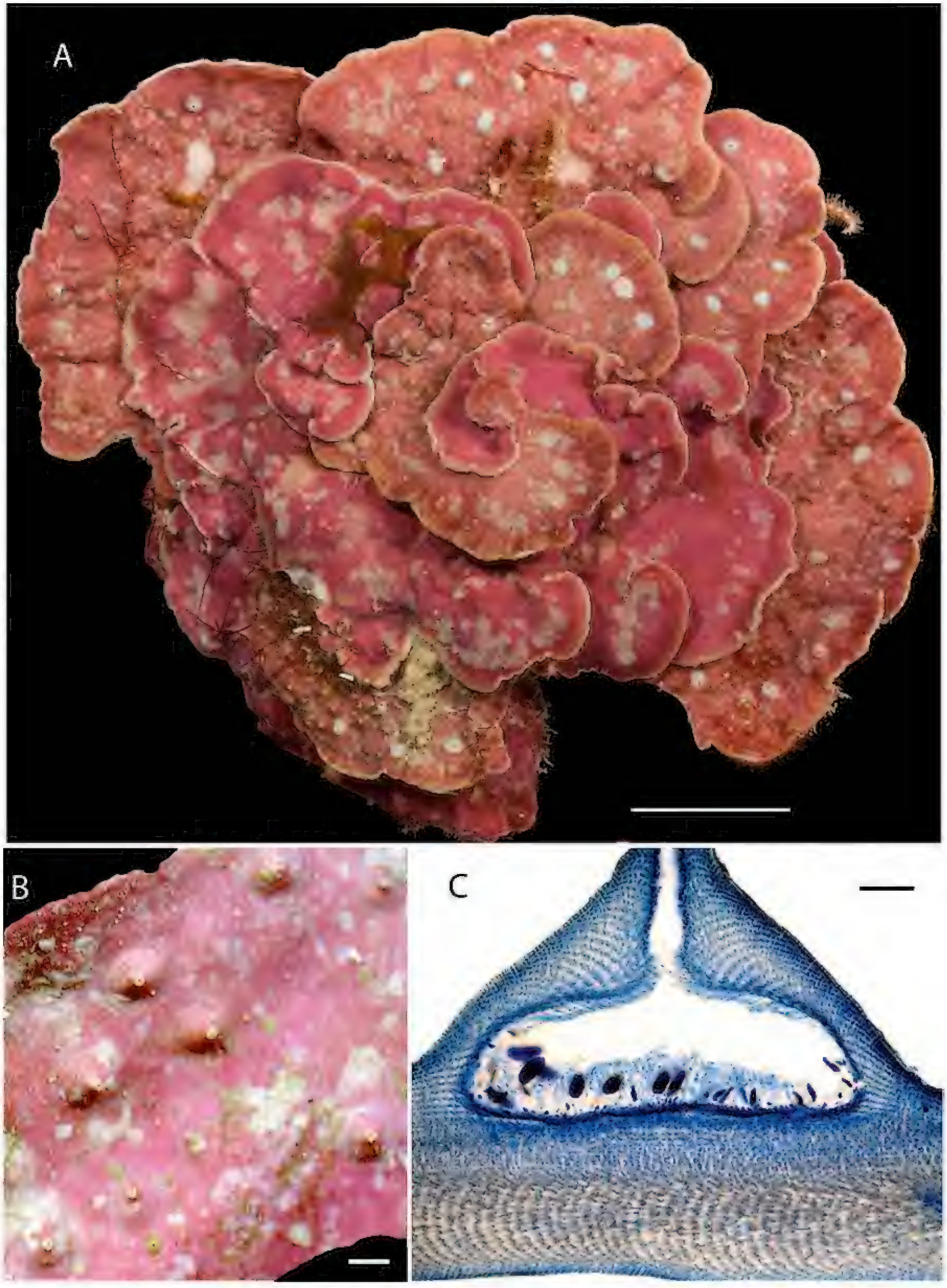

FIGURE 29. *Neogoniolithon solubile*. DLB7940. (A) Herbarium specimen, edge of insular shelf ("Rojos") offshore from La Parguera, 18 m. Scale bar = 1 cm. (B, C) Uniporate tetrasporangial conceptacles. Scale bars = 1 mm and 100 µm, respectively.

2.0 mm (Taylor 1960). Lower branches are frequently anastomosed. Medullary perithallial cells are 12–20 µm broad and 25–40 µm long, bending radially and forming smaller squarish or rectangular cells, 12–18 × 12–25 µm (W × L), where trichocytes are found. Tetrasporangial conceptacles are conical and measure 800 µm diam. Algae are pale pink in color.

Habitat and Comments: Thalli occur as rhodoliths in back reefs to 8.0 m depth (Littler and Littler 2000). Gametophytes have not been reported in the species, and the type material is apparently sterile (Foslie 1901). Mateo-Cid et al. (2014: 90) reported tetrasporangial chamber size as a character distinguishing *N. spectabile* from *N. strictum* (500–800 versus 750–1,000 µm diam.). Specimens collected by Howe from Culebra and Lemon Bay near Guánica are deposited in the Foslie herbarium in TRH (Adey and Lebednik 1967: 29; Woelkerling et al. 2005: 104). [Illustrations: Printz 1929: pl. 49: figs. 1–7; Littler and Littler 2000: 37; Mateo-Cid et al. 2014: figs. 70–74.]

Neogoniolithon strictum (Foslie) Setch. et L.R.Mason

Neogoniolithon strictum (Foslie) Setch. et L.R.Mason 1943: 92.
Basionym: *Goniolithon strictum* Foslie 1901: 14–15.

Puerto Rican Records: As *Goniolithon strictum*: Taylor 1960. As *Neogoniolithon strictum*: Ballantine and Aponte 1997a, 2002a.
Western Atlantic Distribution: Caribbean Mexico, Bahamas, Belize, Cuba, Guadeloupe, Hispaniola, Jamaica, Puerto Rico, U.S. Virgin Islands, Colombia.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Florida.

Heavily calcified thalli are profusely branched, originally saxicolous but generally becoming free-living (occurring as rhodoliths) and forming fragile masses, 10–14 cm broad and 6.0 cm high. Branching is repeatedly loosely subdichotomous with irregular branches spreading and often recurved. Occasionally branches are at right angles to the bearing axes. The branches are terete or sometimes compressed, 1.0–1.5 mm diam. Branching in attached forms is crowded. Medullary perithallial cells are 15–25 µm diam. and 35–55 µm long, bending radially and forming smaller squarish or rectangular cells, 12–20 × 12–25 µm (D × L), where numerous trichocytes are found. Algae are rose red in color.

Habitat and Comments: *Neogoniolithon strictum* generally occurs in intertidal and shallow water at less than 3.0 m depth, commonly found in seagrass beds or reef flats. Bosence (1985) described large-scale mound building formations by *N. strictum* in the Florida Keys. Gametophytes have not been recorded in the species, and the type material is apparently sterile (Foslie 1901). Mateo-Cid et al. (2014: figs. 79, 80) reported conical tetrasporangial conceptacles to project laterally on terminal branches, with pore filaments composed of cells protruding laterally into the canal. The relationship of *N. strictum* to the little-known *Goniolithon decutescens* (Heydr.) M.Howe, here cited as an incertae sedis species (below), requires further investigation. [Illustrations: as *Neogoniolithon strictum*, Bosence 1985: pl. 22: figs. 1–7, pl. 28: figs. 1–8; Littler and Littler 2000: 37; Mateo-Cid et al. 2014: figs. 76–80; as *Goniolithon strictum*, Taylor 1960: pl. 77: figs. 1, 2; Printz 1929: pl. 50: figs. 1–9.]

Porolithoideae A.Kato et Baba in Kato et al.

Porolithon (Foslie) Foslie

Porolithon (Foslie) Foslie 1909: 57.
Basionym: *Lithophyllum* subgenus *Porolithon* Foslie 1906b: 24.
Heterotypic Synonym: Harveylithon A.Rösler, F.Perfectti, V.Peña et J.C.Braga 2016: 424.

Thalli are encrusting, saxicolous, or epizoic, with smooth surfaces (although certain non-Caribbean species produce perithallial protuberances). The hypothallus is polystromatic and non-coaxial, supporting ascending perithallial and descending hypothallial filaments. Cell fusions between contiguous vegetative cells are common; secondary pit connections are lacking. Epithallial cells, 1–4, terminate perithallial filaments and are rounded or flattened but not flared. Trichocytes usually occur among epithallial cells singly, or in horizontal groups, and become embedded in the thallus. Pore cells lining the canal of tetrasporangial conceptacles are orientated perpendicularly to the roof surface. Spermatangial conceptacles develop simple spermatangia on the floor, and carposporangial conceptacles produce carposporangia from the periphery of the fusion cell. Older conceptacles become embedded in the perithallus.

Comments: The generitype *P. onkodes* (Heydr.) Foslie is originally described from collections made at Tami Island, northwest edge of Huon Gulf, Papua New Guinea, and is widely reported in the Indo-Pacific and even the Atlantic coast of Mexico (Mendoza-González et al. 2009). Maneveldt and Keats (2014: 218–230, figs. 5–8, 11) studied lectotype material (TRH A26-1494) and showed the presence of (1) up to 3 rounded epithallial cells, (2) trichocytes in horizontal series, (3) a polystromatic hypothallus composed of at least 2 parallel layers producing short descending filaments and an ascending perithallus, and (4) enlarged pore cells located at the base of the canal of a tetrasporangial conceptacle. They concluded that "pore-canal filaments are orientated more-or-less vertically, and do not project into the pore" (Maneveldt and Keats 2014: 238–239). This character is similar to *Porolithon*, *Hydrolithon*, and *Fosliella*, the latter two genera differing vegetatively mainly in possessing a monostromatic hypothallus.

Rösler et al. (2016: 424) erected *Harveylithon* on a molecular basis for thalli showing a "monomerous thallus," "a plumose ventral core," single trichocytes that may become embedded, and "cells lining the pore canal of tetrasporangial conceptacles oriented perpendicular[ly] to the thallus surface." All these characters occur in the type material of *Porolithon*, *P. onkodes* (Penrose and Woelkerling 1988: 166, "trichocytes

appeared to occur singly," figs. 10–14; Maneveldt and Keats 2014: figs. 3–11), and in other collections referred to this species (Penrose and Woelkerling 1992: figs. 4, 5; Penrose 1996: fig. 119), and therefore, *Harveylithon* requires reinvestigation to find the diagnostic morpho-anatomical features that motivate its molecular position as a distinct genus of the Porolithoideae. Two species of *Porolithon* are here recognized to occur in Puerto Rico.

KEY TO THE *POROLITHON* SPECIES OF PUERTO RICO

1. Thalli up to 1 mm thick, covering other organisms and rocks in shallow reef areas, tetrasporangial conceptacles 150–250 µm diam. . . . . *P. pachydermum*
   Thalli thinner, tetrasporangial conceptacles 73–155 µm diam. . . . . *P. caribaeum*

Porolithon caribaeum (Foslie) Athanas. et D.L.Ballant. comb. nov.

Porolithon caribaeum (Foslie) Athanas. et D.L.Ballant. comb. nov.

Basionym: *Lithophyllum decipiens* f. *caribaeum* Foslie 1906b: 18 (as f. "*caribaea*").

Homotypic Synonym: Lithophyllum caribaeum (Foslie) Foslie 1907a: 22, 1909: 11; *Neogoniolithon caribaeum* (Foslie) W.H.Adey 1970: 8.

Puerto Rican Records: As *Lithophyllum caribaeum*: Taylor 1960. As *Neogoniolithon caribaeum*: Ballantine and Aponte 1997a, 2002a.

Western Atlantic Records: United States (North Carolina), Bahamas, Hispaniola, Jamaica, Puerto Rico, U.S. Virgin Islands.

Type Locality: St. Thomas, U.S. Virgin Islands.

Thalli thin, 75–240 µm thick, adhering closely to pebbles. The surface is smooth, lacking erect protuberances with entire to lobed margins, lacking orbital ridges. The hypothallus is polystromatic and non-coaxial, composed of cells 3.0–8.0 µm broad and 3.0–16 µm long. Ascending perithallial filaments are composed of isodiametric cells, 3.0–7.0 µm diam. Cell fusions are common, and secondary pit connections are absent. Subepithallial cells attain 11 µm in length and are 4.0–6.0 µm diam. Epithallial cells are nearly isodiametric, 3.0–7.0 µm diam. and 3.0–6.0 µm long. Trichocytes occur singly (rarely in pairs) among epithallial cells and measure 5.0–10 µm diam. and 8.0–27 µm in length. Embedded trichocytes are not reported. Tetrasporangial conceptacles are flush with the thallus surface or slightly raised, 73–155 µm in external diameter, with elliptical to spherical chambers, 61–85 µm diam. and 37–66 µm high. The roof is 10–17 µm thick, composed of a palisade cell and 1–2 smaller cells that include the epithallium. A ring of enlarged cells lines the base of canals and is oriented more or less perpendicularly to the roof surface. A columella is lacking. Zonately divided tetrasporangia occur in the periphery of the chamber and measure 25–50 µm in length and 6–34 µm diam. Embedded conceptacles are rare.

Habitat and Comments: In describing the species, Foslie (1906b, 1907a, 1909) gave no information about habitat or collector, and no specimens were cited. The study of his herbarium showed that the original material had been collected by Børgesen at the harbor of St. Thomas between January and March of 1892 (Adey and Lebednik 1967: 14; Woelkerling 1993: 48). Lemoine (in Børgesen 1917: 160) reported several collections of the species in Børgesen's herbarium (C) made either in shallow water in the harbour of Christiansted (St. Croix) or from exposed rocks (Børgesen no. 1468) or from Water Island (St. Thomas) at a depth of about 27 m ("15 brasses," Børgesen no. 1161, in C), and we may assume that material of the last collection was sent to Foslie in TRH to provide the protologue (Foslie 1906b). However, Lemoine (in Børgesen 1917) reported a monostromatic hypothallus in the species, which is at variance with the lectotype (Printz 1929) selected by Adey and Lebednik (1967: 14) and recently studied by Maneveldt et al. (2015). Adey (1970) transferred the species to *Neogoniolithon*, indicating that the hypothallus is polystromatic. Suyemoto (1980) compared an "isolectotype" to material from Onslow Bay (see Schneider and Searles 1991: 242–243) and described monoecious gametophytes with spermatangia restricted to the conceptacle floor and carposporangia produced from the periphery of the fusion cell, thereby providing evidence for the exclusion of the species from *Neogoniolithon*. Maneveldt et al. (2015: 239, figs. 29–35, table 1) reexamined the lectotype in TRH (A1-8) and confirmed the presence of a polystromatic hypothallus and pore cells orientated more or less perpendicularly to the roof surface. These characters support the present transfer of the species to *Porolithon*, and we provide in our species description the essentials of Maneveldt et al.'s (2015) account.

Maneveldt et al. (2015: 242, 243, 250) further considered *P. caribaeum*, *Neogoniolithon erosum* (Foslie) W.H.Adey (type locality: St. Thomas, U.S. Virgin Islands), and *N. rugulosum* W.H.Adey et al. (type locality: Palea Point, Hanauma Bay, Oahu, Hawaii) to be conspecific with *Hydrolithon samoënse* (Foslie) Keats et Y.M.Chamb. (type locality: Satana, Saraii Island, Western Samoa). We think this conclusion is premature because new topotype material was not included in their study, where information from gametophytes is also missing for all putative synonyms. Additionally, perithallial cells in *H. samoënse* may be horizontally elongated to twice their length (Keats and Chamberlain 1994: fig. 37; Maneveldt et al. 2015: fig. 16), a character not reported in the putative synonyms, whereas tetrasporangial conceptacles of *N. erosum* are about twice the size of those of *P. caribaeum*.

Specimens collected by Howe (as *Lithophyllum caribaeum*) from Culebra and Guánica Harbor are deposited in the Foslie herbarium in TRH (Adey and Lebednik 1967: 14). [Illustrations: as *Lithophyllum caribaeum*, Printz 1929: pl. 53: fig. 7; as *Neogoniolithon caribaeum*, Maneveldt et al. 2015: figs. 29–35.]

Porolithon pachydermum (Foslie) Foslie

FIGURE 30

Porolithon pachydermum (Foslie) Foslie 1909: 57.

Basionym: *Lithophyllum onkodes* f. *pachydermum* Foslie 1904a: 5.

Homotypic Synonyms: Lithophyllum pachydermum (Foslie) Foslie 1906a: 22; *Hydrolithon pachydermum* (Foslie) J.C.Bailey, J.E.Gabel et Freshwater 2004: 3.

Puerto Rico Records: As *Porolithon pachydermum*: Taylor 1960; Ballantine and Aponte 1997a, 2002a. As *Hydrolithon pachydermum*: Bailey et al. 2004, 2005.

West Atlantic Distribution: Bahamas, Barbados, Belize, Cuba, Jamaica, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia.

Type Locality: St. Croix(?), West Indies.

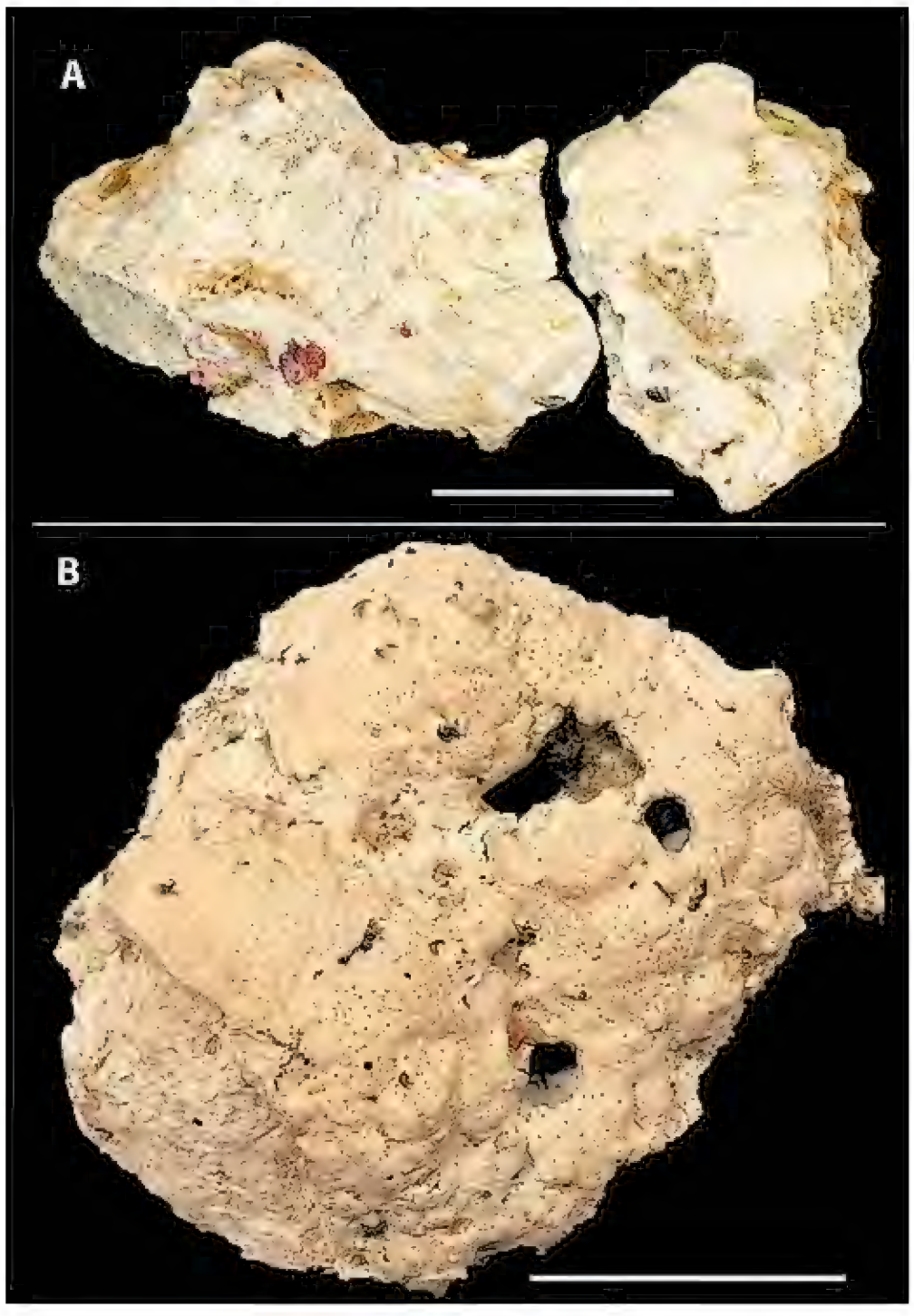

FIGURE 30. *Porolithon pachydermum*. (A) TRH A26-1553, the holotype specimen attached to a conglomerate of dead corals with admixtures, "West Indies," "1848." Scale bar = 2.0 cm. (B) TRH A-1550, herbarium specimen collected at Culebra Island, 3 March 1906, M. Howe no. 4223. Scale bar = 2.0 cm.

Thalli, at least 5.0 cm in extent and up to 1.0 mm thick, encrust hard substrata in the littoral and upper sublittoral, forming a smooth surface lacking perithallial protuberances. The hypothallus is polystromatic and non-coaxial, composed of cells 4.0–10 µm broad and 6.0–9.0 µm long. The perithallus is compact, composed of cells 6.0–9.0 µm broad and 8.0–14 µm long. Trichocytes, 6.0–8.0 µm broad and 17–29 µm long, occur in horizontal groups (roundish patches in view from above) that become embedded in the perithallus. Cell fusions between vegetative cells are common. Secondary pit connections are absent. Carposporangial and tetrasporangial conceptacles are convex, the former 200–300 µm diam. and the latter 150–250 µm diam. and not prominent. Tetrasporangia measure 30–40 µm broad and 60–70 µm long. Older conceptacles become embedded in the perithallus.

Habitat and Comments: *Porolithon pachydermum* is a distinctive, widespread, and very common species in the western Atlantic, forming extensive pavements over reef substrata (Johansen 1981; Littler and Littler 2000; Bailey et al. 2004). Despite its commonness, descriptions of its thallus structure and reproduction are rare. Lemoine (in Børgesen 1917: 180–181) reported smaller vegetative cells and trichocytes in Børgesen's collections from St. John (Cruz Bay; Great Cruz Bay no. 1782) and also cited (without documentation) the remains of the original material (in C) collected by Ørsted in the Danish West Indies (now U.S. Virgin Islands) in 1848. Closer information on the type locality is lacking. In the protologue, Foslie (1904a: 5) distinguished the "vestindiske" f. *pachydermum* from *Lithophyllum onkodes* by the presence of thicker cell walls, and in the same year he speculated its origin to be "St. Croix?" (Foslie 1904b: 59). He later commented that it is weakly distinct from *Lithophyllum onkodes*, differing by thicker cell walls and a less smooth, irregular surface (Foslie 1906a: 22, as *L. pachydermum*). He finally included both species in *Porolithon* on the basis of the presence of trichocytes in groups (Foslie 1909: 57).

Adey (1970: 11) maintained the species in *Porolithon*, a genus characterized by "hypothallial cells parallel to substrate, non-coaxial," and we follow his generic determination, which is generally accepted (e.g., Huisman 2018: 122). Bailey et al. (2004: 8, figs. 1, 2) reported a difference of 6 bp (18S rRNA gene) between an isolate of *P. pachydermum* from Puerto Rico and an isolate of *P. onkodes* from New South Wales (eastern Australia) and proposed the transfer to *Hydrolithon*, neglecting that the type of this genus (*H. reinboldii*) develops a monostromatic hypothallus. Bailey et al. (2004) further suggested a recent splitting between these closely related species (at about 340,000 years ago), supporting Adey's (1979) and Adey et al.'s (1982) thesis that these are sister taxa. The closure of the Panamanian Isthmus at about 3.1 to 5 million years ago (Bornmalm 1992) suggests an older date, whereas Mendoza-González et al.'s (2009) report of both species on the Atlantic coast of Mexico indicates the need for population studies.

The taxonomy of *Porolithon pachydermum* came in dispute when Gabrielson et al. (2018: 430) compared partial DNA

sequences of types and reported that the "holotype" of *Hydrolithon antillarum* and the "lectotype" of *P. pachydermum* "are the same species," which is remotely related to the type of *Porolithon onkodes* (type locality: New Guinea). Gabrielson et al. most likely confirmed the generic distinction between *Hydrolithon antillarum* and *Porolithon onkodes*, but we are skeptical about the proposed synonymy (*H. antillarum* = *P. pachydermum*) because it was based on partial sequences alone without morpho-anatomical comparison of the relevant types or a comparison of sequences of new material.

According to T. Prestø, keeper of the Foslie herbarium in TRH (personal communication, 14 November 2023), the type material of *P. pachydermum* (A26-1553) includes an original Foslie slide and a fragment (~6 cm in extent) presently broken into two pieces (Tâmega et al. 2014: fig. 16; Figure 30A). This fragment is a conglomerate of dead corals embedded in hard substance, externally inhabited by minor algal crusts and bryozoans. Although this material is unambiguously the nomenclatural holotype (Turland et al. 2018: Article 8.2), a representative thallus of *P. pachydermum* is no longer apparent on this fragment, and the presence of admixtures cannot be precluded. From a nomenclatural point of view, further study is needed to document the apparent type element of *P. pachydermum*, which has to be in agreement with the material on the Foslie slide. In the absence of any representative material, neotypification has to be proposed. It is also not apparent where Gabrielson et al. (2018) extracted material for DNA analysis since they did not mark any place on the fragment (T. Prestø, pers. comm.). Hence, the possibility that they analyzed admixtures exists. It should be added that *P. pachydermum* and *H. antillarum* co-occur in the littoral of Puerto Rico at the same time of the year (TRH A27-1565 versus A26-1550). Tâmega et al. (2014: figs. 16, 18, 20, 22) examined the type material and showed the presence of conceptacles, either embedded or flush with the surface, and trichocytes in horizontal series terminating perithallial filaments. However, it is not clear whether their observations were based on the Foslie slide or new sections of the type, and they also failed to provide data for the hypothallus. Two additional slides marked "*Lithophyllum pachydermum*, Bot. Mus. Klehavn 1900" and "Kleanen" exist in the type collection but without other information (Woelkerling et al. 2005:214).

Specimens collected by Howe from Culebra Island and San Juan are deposited in the Foslie herbarium (Adey and Lebednik 1967, as *Lithophyllum pachydermum*). [Additional illustrations: as *Lithophyllum pachydermum*, Printz 1929: pl. 67: fig. 9; as *Porolithon pachydermum*, Littler and Littler 2000: 38–39, 77; as *Hydrolithon pachydermum*, Mendoza-González et al. 2009: figs. 6, 7.]

Spongitis Kütz.

Spongitis Kütz. 1841: 30 (as "*Spongites*").

Thalli are heavily calcified irregular conglomerate masses that are attached or unattached. Individuals are distinctively fruticose and may bear on their thallus other organisms, including attached, epiphytic species of *Neogoniolithon*. Thalli may have boreholes made by animals. The hypothallus is polystromatic, non-coaxial and supports an ascending perithallus lacking stratification. Epithallial cells terminate perithallial filaments and are flattened to roundish. Adjacent cells of vegetative filaments are connected by fusions, and secondary pit connections are absent. Trichocytes are lacking or may occur singly among epithallial cells. Tetra/bisporangial conceptacles are provided with pore cells that protrude laterally into the canal (Penrose and Woelkerling 1992: figs. 6, 7). Spermatangial conceptacles develop simple spermatangia on the floor, and carposporangial conceptacles produce carposporangia from the periphery of the fusion cell. However, reproductive data are based on collections from the Southern Hemisphere (Penrose, 1991; Penrose and Woelkerling 1992: figs. 6, 7), and whether they are compatible with the Mediterranean generitype *S. fruticulosa* Kütz. is uncertain. One species is reported from Puerto Rico.

Spongitis munita (Foslie et M.Howe) Athanas. et D.L.Ballant. comb. nov.

Spongitis munita (Foslie et M.Howe) Athanas. et D.L.Ballant. comb. nov.

Basionym: Lithophyllum munitum Foslie et M.Howe 1906a: 132, pls. 86, 88, 89.

Homotypic Synonyms: Hydrolithon munitum (Foslie et M.Howe) Penrose 1996: 263, fig. 120. *Harveylithon munitum* (Foslie et M.Howe) A.Rösler, F.Perfectti, V.Peña et J.C.Braga 2016: 425, figs. 2, 3.

Puerto Rican Records: As *Lithophyllum munitum*: Taylor 1960; Athanasiadis et al. 2013.

Western Atlantic Distribution: Bahamas, Jamaica, Puerto Rico.

Type Locality: Cave Cays, Exuma Chain, Bahamas.

Thalli are irregular fruticose masses, 3.0–6.0 cm thick, with densely crowded wartlike protrusions or with sparingly and irregularly divided branches, 2.0–4.0 mm diam. and to 4.0 mm tall. The branches sometimes anastomose. The irregularities are accounted for in part by the enclosure of other organisms, showing numerous bore holes caused by animals, and in part by being intermingled or superposed by other Spongitidaceae (*Neogoniolithon strictum?*). The hypothallus is polystromatic, and cells measure 5.0–8.0 µm diam. and 12–24 µm long. The perithallus is composed of subquadrate or rounded cells, 5.0–9.0 µm diam., shorter or longer (to 11 µm) when viewed in vertical section. Cell fusions between contiguous vegetative cells are common, and secondary pit connections are absent. Trichocytes are lacking. Uniporate conceptacles are slightly convex, measuring about 300 µm diam., and become embedded in the perithallus. Algae are brownish red when living.

Habitat and Comments: The original and only collection cited in the protologue grew on a coarse dead coral near the low-water mark under shelving rocks, and our account above is based on the protologue and a study of type specimens in PC and NY (Richards et al. 2021) that demonstrate a fruticose habit and the lack of trichocytes in the species. No other confirmed records

exist, and in the absence of reproductive characters the generic position in *Spongitis* is tentative. The original collection apparently included several specimens presently deposited in NY, TRH, BM, and PC (Woelkerling 1993; Richards et al. 2021). Howe (1920b) reported *Lithophyllum munitum* from the Bahamas and Jamaica but gave no account. Adey and Lebednik (1967: 20) typified the species with Howe's material in TRH (Printz 1929), and Woelkerling et al. (2005: 49) restricted their (lecto)typification to the single specimen illustrated by Printz (1929) (TRH A4-221). The second specimen in TRH (Printz 1929) is annotated "Howe no 4023b" (Woelkerling et al. 2005: 49, A4-222). Richards et al. (2021: fig. 4A–C) examined type specimens in PC and NY and illustrated the presence of a polystromatic hypothallus and cell fusions and apparent lack of both trichocytes and secondary pit connections. The nature of the uniporate conceptacles (whether gametangial or bi/tetrasporangial) described in the protologue remains unknown.

Penrose (1996) and Harvey et al. (2006) provided detailed accounts of "*Hydrolithon munitum*" from southern and southeastern Australia, but their specimens differ both in habit (being encrusting and lacking protuberances) and in possessing abundant trichocytes. In both Australian accounts, the hypothallus was polystromatic, spermatangia were simple and restricted to the conceptacle floor, carposporangia developed from the periphery of the fusion cell, and pore cells of tetrasporangial conceptacles projected perpendicularly inside the canal, indicating that the material rather belonged to *Porolithon*.

Richards et al. (2021, as *Harveylithon munitum*) expanded the taxonomic status of the species, including thalli with "smooth or warty surface" and "trichocytes borne singly . . . occasionally in pairs . . . or clusters." They also proposed synonymy with *Neogoniolithon accretum* and *N. affine* after comparing partial sequences from type specimens in NY and PC. We are skeptical of this conclusion since the fruticose thallus of the lectotype and all syntypes of *Spongitis (Lithophyllum, Harveylithon) munita* (Printz 1929; Richards et al. 2021: fig. 4) contrast markedly with the smooth surface of the holotype and all illustrated reports of *Neogoniolithon (Goniolithon) accretum* (Foslie and Howe 1906a: 131, pl. 85: fig. 2; Printz 1929: pl. 45: figs. 19, 20; **Masaki** 1968: pl. 33; Mateo-Cid et al. 2014: fig. 2). We have previously been critical of genetic results based on partial sequences alone (Athanasiadis 2020; Athanasiadis and Ballantine 2024) and consider that the proposed synonymy is pending confirmation.

The present transfer of *Lithophyllum munitum* to *Spongitis* is based on characters of habit (being rather similar to the Mediterranean generitype *S. fruticulosa*), internal structure (polystromatic hypothallus, cell fusions, embedded conceptacles), and the lack of trichocytes, which agrees with Basso and Rodondi's (2006) study of the lectotype and new Mediterranean material.

Specimens collected by Howe from Culebra Island are deposited in the Foslie herbarium (Adey and Lebednik 1967: 20, as *Lithophyllum munitum*). [Illustrations: as *Lithophyllum munitum*, Foslie and Howe 1906a: pls. 86, 88, 89; Printz 1929: pl. 56: figs. 16, 17; Richards et al. 2021: fig. 4A–C.]

Incertae Sedis

Goniolithon strictum var. *nanum* Foslie et M.Howe

FIGURE 31

Goniolithon strictum var. *nanum* Foslie et M.Howe 1906a: 131, pl. 82: fig. 1.

Homotypic Synonyms: Lithophyllum strictum var. *nanum* (Foslie et M.Howe) Me.Lemoine in Børgesen 1917: 164 (as "*nana*"); *Goniolithon spectabile* f. *nanum* (Foslie et M.Howe) Foslie in Printz 1929: pl. 49: figs. 8–11 (as f. "*nana*"); Taylor 1960: 399 (as f. "*nana*"); *Goniolithon spectabile* f. *nanum* (Foslie et M.Howe) Printz 1929: 31 (as f. "*nana*"), nom. illeg.

Puerto Rican Records: As *Goniolithon spectabile* f. *nanum*: Printz 1929. As *Goniolithon strictum* var. *nanum*: Taylor 1960.

Western Atlantic Distribution: Puerto Rico, St. Croix (U.S. Virgin Islands), Florida, Hispaniola.

Type Locality: San Juan, Puerto Rico.

Thalli form an encrusting base with erect sub-fastigiate, terete, or sub-compressed crowded branches, 0.8–1.0 mm diam., mostly 5.0–10 mm high. Otherwise as in the autonym.

Habitat and Comments: *Goniolithon strictum* var. *nanum* was originally collected at San Juan "mostly in shallow tide-pools," and seven specimens were illustrated in the protologue (cited above; Foslie and Howe 1906a: pl. 82: fig. 1, Howe no. 2235). Foslie and Howe commented that it is a delicate form corresponding to *Goniolithon frutescens* f. *subtile* Foslie (1904b: 53, "*subtilis*," pl. 10: figs. 12, 13) and possibly identical to it, "as it is not altogether certain that the Atlantic *G. strictum* can be kept separate from the Pacific *G. frutescens*."

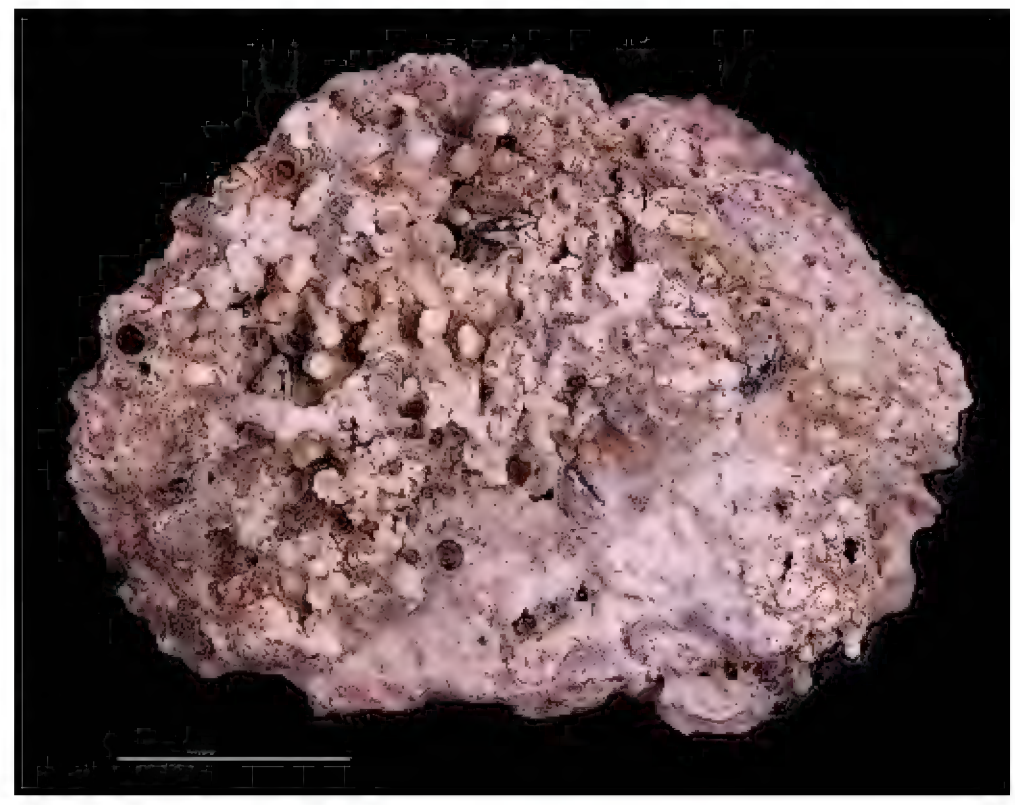

FIGURE 31. *Goniolithon strictum* var. *nanum*. TRH A13-700, habit of the lectotype. Scale bar = 4.0 cm.

Following Foslie's unpublished annotations in TRH, where the epithet *strictum* is replaced with *spectabile* and the name *nanum* is preceded by the rank of forma (Woelkerling et al. 2005: 104), Printz published the name *Goniolithon spectabile* f. *nanum* Printz (1929: 31, as "*nana*"), attributing the combination to Foslie in the plates (Printz 1929: pl. 49: figs. 8–11). Printz gave no reference to Foslie and Howe (1906a), but it is clear that he followed Foslie's herbarium annotations, "and [since] a potential basionym applying to the same taxon exists" (Turland et al. 2018: Article 41.4), the new combination *G. spectabile* f. *nanum* (Foslie et M.Howe) Foslie in Printz is valid (Woelkerling 1993: 156). We follow Taylor (1960) in citing the correct authorship under *Goniolithon spectabile* f. *nanum*.

Taylor (1960: 399) recognized both *Goniolithon strictum* var. *nanum* (citing the protologue) and *Goniolithon spectabile* f. *nanum* Foslie (most likely referring to Printz 1929). He also provided an illustration (Taylor 1960: pl. 78: fig. 1) and the following description for the latter name: "Cushions small, 2.0–3.0 cm. diam., the branches more of less densely packed, 0.75–1.0 mm diam."

Since it is clear from the study of Foslie's collections in TRH (Woelkerling 1993: 156; Woelkerling et al. 2005: 104) that *G. strictum* var. *nanum* Foslie et M.Howe (1906a: 131) and *G. spectabile* f. *nanum* (Foslie et M.Howe) Printz (1929) are based on the same type, Taylor's *Goniolithon spectabile* f. *nanum* most likely refers to the same entity.

Printz (1929: pl. 49: fig. 8, "the type") typified f. *nanum* with a specimen from Howe's collection no. 2235 in TRH (A13-700). His lectotypification was overlooked by later authors, who considered that the "holotype" should be in NY (Woelkerling 1993; Woelkerling et al. 2005). Taxonomically, *Goniolithon strictum* var. *nanum*, with its much narrower branches, 0.8–1.0 mm in diameter, differs from the autonym that has wider branches, (1.5–)2.0–3.0(–5) mm diam.

We reexamined the lectotype (Printz 1929: pl. 49: fig. 8) and could confirm the diagnostic characters of var. *nanum*, which also differs from young specimens of *Melyvonnea erubescens* by its thinner and shorter branches—those of *M. erubescens* being simple or divided, to 30 mm long and 5 mm broad (Athanasiadis and Ballantine 2014: 414). Upon examination of the Foslie slide (annotated "Gon. strictum f. nana 2235 leg.M.A.Howe") included in the lectotype collection (TRH A13-700), the erect branches were shown to be ~1.0 mm diam. and ~6 mm high, composed of stratified perithallial cells, 20–45 × 15–20 µm (L × W), bending outward and occasionally provided with terminal trichocytes, 40–50 × 20–30 µm (L × W). Present data suggest that var *nanum* belongs to the genus *Neogoniolithon*, but gametophytes and tetrasporophytes remain to be described before it can be recognized as a distinct variety of *N. strictum* or acquire a separate species status. Since the protologue, var. *nanum* has been recorded from a wide range of localities in the Caribbean (Lemoine in Børgesen 1917, Lemoine 1924; Taylor 1928, 1960).

Specimens collected by Howe at San Juan are deposited both in NY and in the Foslie herbarium in TRH (Adey and Lebednik 1967: 30, as *Goniolithon spectabile*). [Additional illustration: as *Goniolithon strictum* var. *nanum*, Foslie and Howe 1906a: pl. 81: fig. 1; as *Goniolithon spectabile* f. *nanum*, Printz 1929: pl. 49: figs. 8–11; Taylor 1960: pl. 78: fig. 1.]

Goniolithon decutescens (Heydr.) Foslie ex M.Howe

Goniolithon decutescens (Heydr.) Foslie ex M.Howe 1918a: 538.
Basionym: Lithothamnion decutescens Heydr. 1901: 541, pl. 11: fig. 7.
Puerto Rican Records: As *Goniolithon decutescens*: Ballantine and Aponte 1997a, 2002a; Dawes and Mathieson 2008.
Western Atlantic Distribution: Panama, United States (Florida), Bahamas, Bermuda, Hispaniola, Puerto Rico, Tobago, Turks and Caicos, U.S. Virgin Islands.
Type Locality: Bermuda.

Thalli are attached to the substratum (rock?) by an inconspicuous basal disk, producing an erect frond to 8.0 cm high and 9.0 cm broad composed of ramified branches. Branches initiate at a distance of 0.5–1.0 cm from each other and are ~3.0 mm thick at their base, becoming thinner, ~1.0 mm, at their apex, where they are irregularly dichotomously divided, about 1.0–1.5 cm below their tips, with rather long distances between dichotomies. The species resembles in habit *Lithothamnion* (now *Lithophyllum*) *tamiense* Heydrich (1897c: 1, pl. 1: figs. 4–7) described from Papua New Guinea. The hypothallus is composed of cells, up to 32 µm long and 20 µm broad, and the perithallus is composed of cells ~12–14 µm diam. Trichocytes are 30 µm broad and 40–60 µm long.

Comments: No information of habitat was provided in the protologue (cited above), and the single illustration (Heydrich 1901: pl. 11: fig. 7) shows a well-ramified thallus (said to reach the size of a fist) that comes close to *Neogoniolithon strictum*. Woelkerling and Lamy (1998: 339) located the holotype in PC and reported that it is sterile. This questions even the family position of the species given Heydrich's (1901) suggestion that the species is related to *Lithophyllum tamiense* (Heydrich) Verhej. However, similarly branched species of *Lithophyllum* are not reported in the western Atlantic. Foslie (1907a: 19) considered *Lithothamnion decutescens* to be the correct name of *Goniolithon spectabile* Foslie, but he nevertheless maintained the binomial *G. spectabile* (Foslie 1907a). Howe (1918a) accepted *Goniolithon decutescens* to include *G. spectabile* and also noted that the "*G. decutescens-G. strictum* group" is widely and frequently represented in the West Indian region. He later suggested that even *Goniolithon rhizophorae* Foslie et M.Howe and *G. strictum* var. *nanum* Foslie et M.Howe should be included in the above synonymy (Howe 1920b: 586, with reservation).

Following Howe (1920b), Taylor originally attributed the name *G. decutescens* to fruticose crusts with short protuberances to 1.0 cm long (Taylor 1928: pl. 36: fig. 3), but he later

recognized this material as *G. strictum* var. *nanum* (Taylor 1960: pl. 78: fig. 1). Taylor (1960) maintained *G. decutescens* as a distinct species characterized by a "most prominent" crustose portion, but the protologue describes a minimal basal disk (Heydrich 1901, "sehr geringer Basalsheibe"). In a review of the genus *Neogoniolithon* from Mexico, Mateo-Cid et al. (2014) recognized 14 species (4 unnamed) and considered *G. decutescens* to be closely related to *N. siankanense* Mateo-Cid et al. (validated in Mateo-Cid et al. 2020)—the latter species said to have a basal layer 400–500 µm thick and thinner branches, 1.0–1.5 mm thick, "essentially uniform in diameter along their entire length and trichotomous, irregularly subdichotomous or anastomosing . . . [and] often terminat[ing] in conical to dome-shaped conceptacles" (Mateo-Cid et al. 2014: 74).

Following Foslie (1907a), Howe (1918a), and the Puerto Rican records, *Goniolithon decutescens* should be transferred to *Neogoniolithon*, material of which is deposited in PC with some fragments in TRH (Woelkerling et al. 2005: 101–102). Present morpho-anatomical data suggest that this species is an attached form, related to *N. strictum*, but study of fertile collections is required before its recognition. [Illustration: as *Lithothamnion decutescens*, Heydrich 1901: 541, pl. 11: fig. 7.]

Neogoniolithon affine (Foslie et M.Howe) Setch. et L.R.Mason

Neogoniolithon affine (Foslie et M.Howe) Setch. et L.R.Mason 1943: 91.
Basionym: Goniolithon affine Foslie et M.Howe in Foslie 1907b: 22–23.
Puerto Rican Records: Setchell and Mason 1943; Taylor 1960; Ballantine and Aponte 1997a, 2002a.
Western Atlantic Distribution: Puerto Rico.
Type Locality: Culebra Island, Puerto Rico.

Thalli are 2.0–3.0 cm diam. and ~1 cm thick, forming originally 1.0–2.0 mm thick, almost flat crusts overgrowing small stones. With further development, crusts become thicker and develop warty excrescences or short, closely borne, partly coalescent branches, ~5.0 mm long and 2.0–4.0 mm thick, that often are roundish and depressed in the tips. Tetrasporangial conceptacles are subconical, low, 200–400 µm diam. The tetrasporangia, 50–70 µm long and 20–25 µm broad, are cleaved into four spores. In vertical sections the hypothallus forms few cell layers that in part are radiating, composed of cells 14–25 µm long and 9.0–11 µm broad. Perithallial cells are subsquarish, roundish, or vertically elongate, 7.0–11 µm long and 6.0–9.0 µm broad; they form a vague stratification. Heterocysts (trichocytes) occur very rarely. *Neogoniolithon affine* resembles *Gon.* [*Hydrolithon*] *boergesenii* in habit. It differs, however, by its polystromatic hypothallus and distinctive perithallial cells. The conceptacles are also slightly smaller. The conceptacles ultimately become substantially overgrown by new tissue. The alga occurs close to the low-water level, and specimens collected at Culebra Island bore mature sporangia at the beginning of March (Howe no. 4234).

Habitat and Comments: *Neogoniolithon affine* is known only from the protologue (translated above). Lemoine (in Børgesen 1917: 151) cited the species as "*Lithophyllum affine* Porto-Rico" (invalid comb.) and reported its absence from "Antilles Danoise." Printz (1929: pl. 52: fig. 11) illustrated a single specimen deposited in TRH that was later selected as the (lecto)type by Adey and Lebednik (1967: 28). Setchell and Mason (1943: 90–91) transferred the species to *Neogoniolithon*, placing it within the group "Verrucosae aut ramosae." Taylor (1960) repeated data from the protologue. No later records exist, but *N. affine* has been included in checklists from Puerto Rico.

Richards et al. (2021: fig. 6A–F) studied a NY "fragment removed from the holotype, TRH-A12–622," but failed to provide a Howe number or how (if) the NY material fits the lectotype as described by Foslie (1907b) and illustrated by Printz (1929). Moreover, the morpho-anatomical data illustrated for the NY material (Richards et al. 2001: fig. 6) include the development of plenty of terminal trichocytes (up to five in a series) and conceptacles ~200 µm in external diameter, characters that do not agree with the protologue, where trichocytes are said to be "meget sparsamt" (very rare) and conceptacles to range between 200 and 400 µm diam. Moreover, Richards et al. (2021) proposed synonymy with *Spongitis (Harveylithon) munita* on the basis of a comparison of partial sequences. We consider that the proposed synonymy requires confirmation based on a study of the relevant types and new topotype material. The only authentic material of *N. affine* is in TRH (Printz 1929: pl. 52: fig. 11; Adey and Lebednik 1967: 28; Woelkerling 1993: 21; Woelkerling et al. 2005: 95), but the annotation "NYBG 4234" on the lectotype suggests that a duplicate (with the same Howe number) is deposited in NY.

In the absence of a consensus, the generic position of *N. affine* requires clarification. Assuming that the NY fragment studied by Richards et al. (2021: fig. 6A–F) is authentic, the presence of cell fusions and abundant trichocytes in series suggest a position in *Porolithon* or *Neogoniolithon*, whereas the warty thallus in combination with rare trichocytes (as described in the protologue) suggest an affiliation with *Spongites*. [Illustrations: as *Goniolithon affine*, Printz 1929: pl. 52: fig. 11.]

Rhodogorgonales Fredericq, J.N.Norris et Pueschel[4]

Rhodogorgonaceae Fredericq, J.N.Norris et Pueschel

Renouxia Fredericq et J.N.Norris

Renouxia Fredericq et J.N.Norris 1995: 329.

Thalli are flaccid, lubricous, and lobed. Algae are composed of loose masses of interconnected assimilatory filaments bearing

[4] Contributed by D. L. Ballantine, J. N. Norris, and H. Ruiz.

rhizoidal filaments. Assimilatory filaments are indeterminate and branch pseudodichotomously. Apical cells are dome shaped and densely pigmented. Calciferous cells, surrounded by calcite husks, borne on assimilatory filaments, are short. Gametophytes are dioecious. Gonimoblast filaments are formed directly from the carpogonium and are diffusely branched, branching unilaterally among assimilatory and rhizoidal filaments. Sporangia (carpotetrasporangia?) are irregularly zonately divided.

One of the two known *Renouxia* species occurs in Puerto Rico.

Renouxia antillana Fredericq et J.N.Norris

FIGURE 32

Renouxia antillana Fredericq et J.N.Norris 1995: 329, figs. 1–42.
Puerto Rican Records: Ballantine et al. 2004.
Western Atlantic Distribution: Guadeloupe, Puerto Rico.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Ilet à Caret (between Grande Terre and Basse Terre), Grand Cul de Sac Marin, Guadeloupe.

Renouxia antillana is the type species of the genus. Thalli are very soft and gelatinous, possessing a discoid holdfast, above which is a short, 2.0–5.0 cm wide, stipe. The entire thalli are up to 12 cm tall and consist of few to many irregular compressed lobes, 4.0–7.0 mm thick. Thalli are composed of assimilatory filaments that bear calciferous cells and rhizoidal filaments. The assimilatory filaments possess cells measuring 5.0–8.0 µm diam. and 15–25 µm long. They terminate in dome-shaped apical cells, 5.0 µm diam. and 15–25 µm long. Calciferous cells are 4.0–8.0 µm diam. and 25–30 µm long. Rhizoidal filaments measure 2.5–3.0 µm diam. Carpogonial branches are 2-celled, with the hypogynous cells 8.0 µm broad and 25–45 µm long and the carpogonia 8.0 µm broad and 20 µm long. Carposporangia measure 10–20 µm broad and 30–35 µm long. Purported carpotetrasporangia measure 16 µm broad and 35 µm long. Algae are chalky white in color with pinkish margins.

Habitat and Comments: *Renouxia antillana* is rare in its overall distribution and is not common in the waters surrounding Puerto Rico, where it has been collected at offshore algal plains as well as at the insular shelf edge. [Additional illustration: Ballantine et al. 2004: fig. 1.]

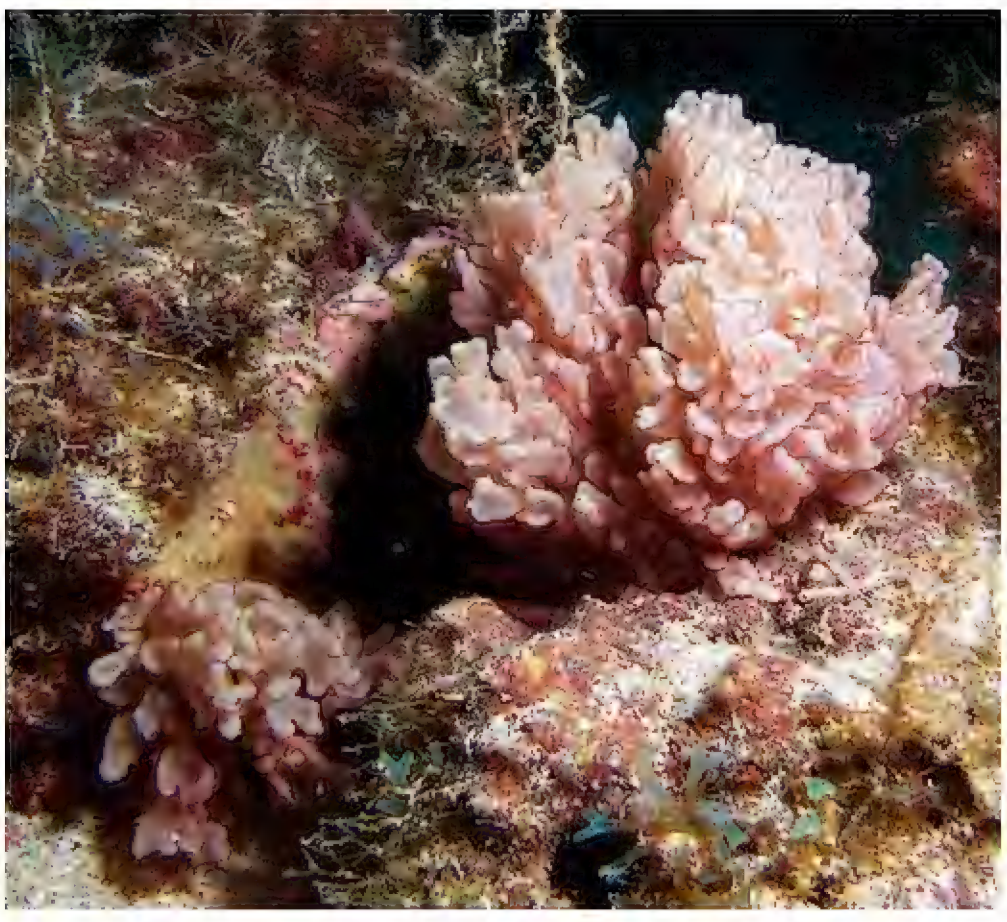

FIGURE 32. *Renouxia antillana*. In situ habit photograph, edge of insular shelf. Field is approximately 15 cm.

Rhodogorgon J.N.Norris et Bucher

Rhodogorgon J.N.Norris et Bucher 1989: 1053.

Cartilaginous thalli are erect, slippery, and lightly calcified. Thalli arise from a small discoid holdfast, with a short stipe and terete to compressed axes. Algae are structurally multiaxial, with a medulla of hyaline intertwined rhizoidal filaments and a cortex comprising fascicles of pigmented cells. Branching is sparse to dense, to several orders, mostly irregularly alternate or radial, occasionally pinnate and secund toward the apices. Elongate undivided calciferous cells form in the cortex and are distally surrounded by a calcite husk. Monosporangia arise at midcortex. Spermatangia are borne in continuous zones, the parent cells arising bilaterally on subterminal cells of cortical filaments, each cutting off a single spermatangium. There are two recognized species of the genus, of which one occurs in Puerto Rico.

Rhodogorgon ramosissima J.N.Norris et Bucher

FIGURE 33

Rhodogorgon ramosissima J.N.Norris et Bucher 1989: 1059, figs. 6, 7.
Puerto Rican Records: Ballantine and Aponte 2002a; Ballantine et al. 2002b.
Western Atlantic Distribution: United States, Antigua, Bahamas, Cuba, Martinique, Puerto Rico, U.S. Virgin Islands, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Carlisle Bay, Antigua, Lesser Antilles.

Thalli are erect, to 50 cm tall from a small discoid holdfast, with a short stipe and terete to compressed axes. Thalli are cartilaginous, slippery, and locally lightly calcified. Medullary filaments are slender, to 4.0 µm diam. and 90 µm long. Cortical filaments measure 70–105 µm diam. Branching is sparse to dense, to several orders, mostly irregular or alternate or radial, occasionally pinnate, secund toward the apices. Algae are whitish pink to red. Two species of the genus are recognized worldwide, one of which is known from Puerto Rico.

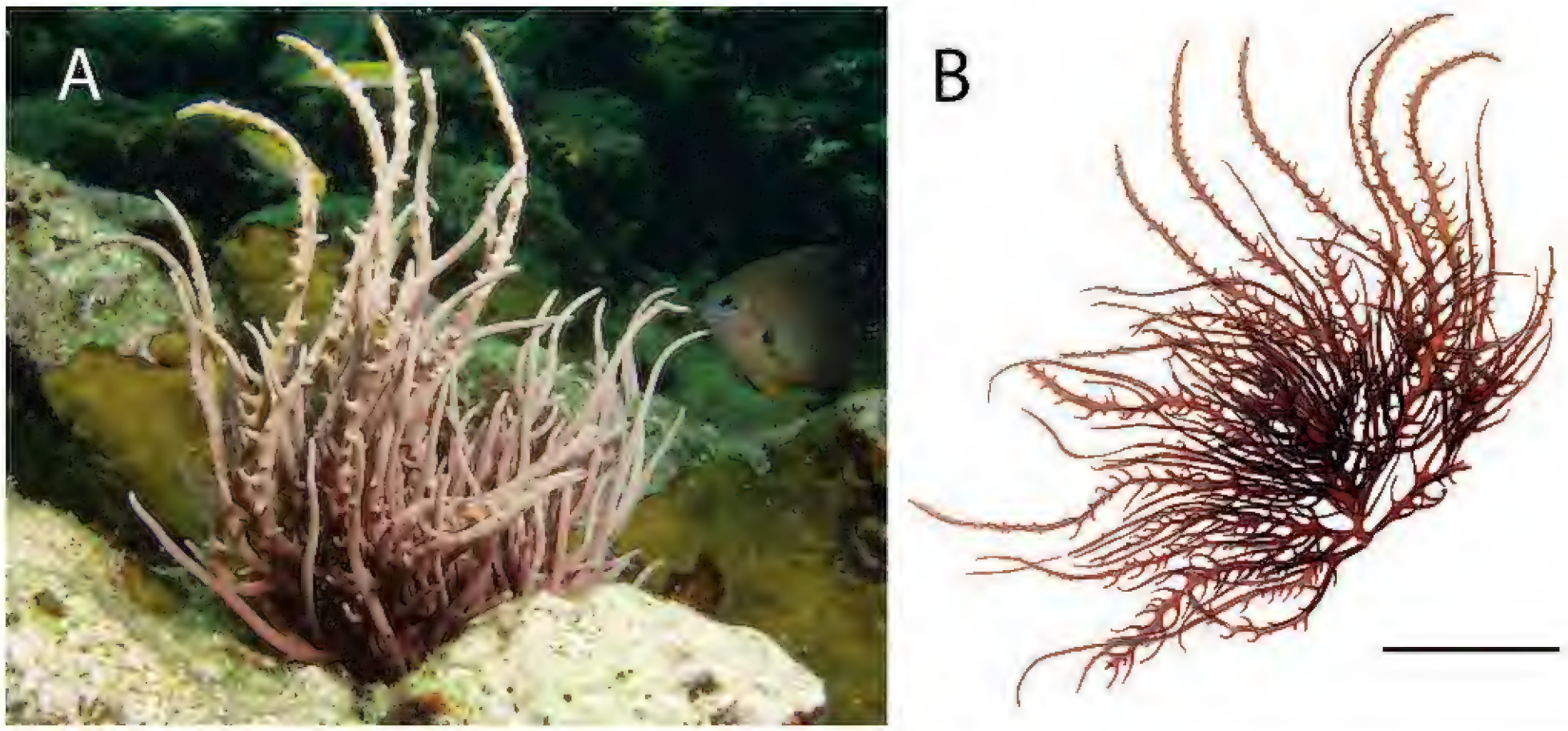

FIGURE 33. *Rhodogorgon ramosissima.* (A) In situ habit photograph, Turrumote Reef, La Parguera, 6.0 m. Field is approximately 20 cm. (B) DLB6037, herbarium specimen, La Pelotas Reef, La Parguera, 2.0 m. Scale bar = 5.0 cm.

Habitat and Comments: *Rhodogorgon ramosissima* is known from shallow to moderate depths, usually in coral reef habitats. The species is never abundant in Puerto Rico and has been collected only sporadically. Branching of Puerto Rican thalli exhibited substantial variation, ranging from opposite to secund and being tight and compact to loose and sparse. It was primarily on the basis of branching variability that led Ogden (1992) to treat *R. carriebowensis* J.N.Norris et Bucher (the generitype) and *R. ramosissima* as conspecific.

Sporolithales Le Gall et G.W.Saunders[5]

Sporolithaceae Verheij

Sporolithon Heydr.

Sporolithon Heydr. 1897b: 66.

Thalli form attached or unattached crusts (rhodoliths) with or without perithallial protuberances. Thallus organization is dorsiventral, composed of a polystromatic hypothallus supporting gradually ascending perithallial filaments that terminate in a layer of flattened and flared epithallial cells. Cell fusions are common between contiguous vegetative cells, and secondary pit connections are sometimes present. Trichocytes are lacking. Gametophytes display characters similar to *Lithothamnion* (Corallinales). Subspherical tetrasporangia are decussately or cruciately divided and occur within uniporate chambers arranged in irregular sori on the thallus surface. Bisporangia are lacking. Thirty-five species of *Sporolithon* are currently recognized, of which one is known from Puerto Rico.

[5] Contributed by A. Athanasiadis, D. L. Ballantine, J. N. Norris, and H. Ruiz.

Sporolithon dimotum (Foslie et M.Howe) Yam.-Tomita ex M.J.Wynne

Sporolithon dimotum (Foslie et M.Howe) Yam.-Tomita ex M.J.Wynne 1986: 2258.

Basionym: Archaeolithothamnion dimotum Foslie et M.Howe 1906a: 128, pl. 80: fig. 1, pl. 87.

Puerto Rican Records: Ballantine and Aponte 1997a, 2002a; Bahia et al. 2011; Richards et al. 2017. As *Archaeolithothamnion dimotum*: Foslie and Howe 1906a; Printz 1929; Taylor 1960.

Western Atlantic Distribution: Bahamas, Bermuda, Hispaniola, Jamaica, Puerto Rico, Brazil.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Lemon Bay, near Guánica, Puerto Rico.

Encrusting thalli closely adhere to the substratum, spreading at least 6.0 cm across and 0.5 to 1.0 mm thick. They lack perithallial protuberances but are provided with thallus projections, which reflect the irregularities of the substratum underneath. The perithallus is composed of partly subsquare cells, 6.0–11 µm diam., partly vertically elongated to 15 µm and occasionally horizontally elongated. Minute intermediate cells are rather numerous. Tetrasporangia are 40–60 µm diam. and 70–85 µm long, with an apical projection (plug?) 15–25 µm long.

Habitat and Comments: Foslie and Howe (1906a: 129) reported the species "on rocks at low-water mark," as maintained by Taylor (1960: 378) for thalli from Hispaniola (Lemoine 1924: 36), Jamaica and Bahamas (Howe 1920b: 584). Howe (1920b: 584) added that the species forms "rather smooth crusts on the older parts of living corals." A later collection from 60 m depth in Brazil was synonymized with "*Sporolithon ptychoides* Heydr.," but it was shown that this material develops pore plates (Bahia et al. 2011: fig. 6), rather than sori, and hence, it should be related to *Corallinapetra* Nelson et al. (2015). Nevertheless, aggregation of tetrasporangial chambers in sori (of irregular shape and indefinite size), although generally attributed to the genus (e.g., Woelkerling 1988: 203; Townsend et al. 1995: 89, fig. 7A), is neither documented in the generitype *S. ptychoides* (Woelkerling 1988) nor shown in *S. dimotum* (Bahia et al. 2011: figs. 9–13). Regarding the original material, the protologue (cited above) was based on a single collection (Howe no. 2667), and one specimen was illustrated (Foslie and Howe 1906a: pl. 80: fig. 1). Printz (1929: pl. 43: fig. 16) illustrated a "part of the plant," but there is no statement that the entire original material was a single (divided) specimen (cf. Foslie and Howe 1906a: 128), and we have to conclude that the original collection included at least two specimens. Adey and Lebednik (1967: 84) selected as the lectotype the TRH specimen illustrated by Printz (1929: pl. 43: fig. 16). Richards et al. (2017: 1053) showed that a partial *rbc*L sequence (263 bp) from a NY type specimen was unique among all other deposited sequences in GenBank, alluding that *S. dimotum* is a distinct species whose relationships are pending further comparative studies. [Illustrations: Bahia et al. 2011: figs. 9–13; as *Archaeolithothamnion dimotum*, Foslie et Howe 1906a: 128, pl. 80: fig. 1, pl. 87; Printz 1929: pl. 43: fig. 16.]

Hildenbrandiophycidae G.W.Saunders et Hommers.[6]

Hildenbrandiales Pueschel et K.M.Cole

Hildenbrandiaceae Rabenh.

Hildenbrandia Nardo

Hildenbrandia Nardo 1834: 675 (as "*Hildenbrandtia*").

Noncalcified crustose thalli are prostrate and leathery in texture. The crusts possess a smooth surface. Algae are totally adherent to the substratum and lack rhizoids. The thallus organization is heterotrichous, and the hypothallus gives rise to the vertical, sparsely branched filaments of the perithallus. Adjacent perithallus cells form secondary pit connections. Perithallial cells are cylindrical, averaging about 5.0 µm diam. Gametophytes are unknown. Tetrasporangia are formed in pitlike conceptacles scattered over the thallus surface. Spherical or cylindrical conceptacles possess an ostiole. The tetrasporangia are zonately divided. Of 18 species recognized worldwide, a single species is known from Puerto Rico.

Hildenbrandia rubra (Sommerf.) Menegh.

Hildenbrandia rubra (Sommerf.) Menegh. 1841: 426.
Basionym: *Verrucaria rubra* Sommerfelt 1826: 140.
Heterotypic Synonym: Hildenbrandia prototypus Nardo 1834: 676 (as "*Hildenbrandtia*").
Puerto Rican Records: As *Hildenbrandia rubra*: Ballantine and Aponte 1997a. As *Hildenbrandia prototypus*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983.
Western Atlantic Distribution: Costa Rica, Panama, United States (Maine, New Hampshire, Connecticut, Florida), Cuba, Jamaica, Hispaniola, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela, Uruguay.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Nordland, Norway.

Thalli are thin, 0.2–0.5 mm thick, and small to very large, expanding to an indefinite extent. Hypothallus cells occur in parallel rows and give rise to vertical perithallus filaments whose cells are 4.0–6.5 µm diam. Uniporate sporangial conceptacles are up to 100 µm diam., and tetrasporangia are 9.0–14 µm diam. and 16–30 µm long. Algae are rose red or brownish red in color.

Habitat and Comments: *Hildenbrandia rubra* occurs on rocks and stones in tide pools or exposed to wave splash. The presence of the species in Puerto Rico is based on the 1963 Díaz-Piferrer report of occurrence as an epizoophyte on the mollusk *Cittarium pica* L. intertidally at Playa Tamarindo, Guánica. [Illustrations: Littler et al. 2008: 24; Braune and Guiry 2011: fig. 124.2.]

Nemaliophycidae T.A.Chr.

Acrochaetiales Feldmann

Acrochaetiaceae Melch.

Acrochaetium Nägeli

Acrochaetium Nägeli in Nägeli and Cramer 1858: 532.

Thalli consist of uniseriate filaments, growing erect or prostrate, frequently occurring as epiphytes and occasionally as endophytes. Erect species are normally less than 5.0 mm high, and cells are generally less than 12 µm diam. Cells possess a single stellate plastids and a central pyrenoid. Branching is irregular, secund, or opposite. In species where sexual reproduction is known, spermatangia occur in small clusters, and carpogonia are sessile on pedicels. Fertilized carpogonia develop directly (there is no auxiliary cell), and they give rise to several carpospores. Tetrasporangia are cruciately divided. Monosporangia occur in gametophytic and sporophytic thalli. In many species the only form of propagation known is via monospores.

[6] Contributed by D. L. Ballantine, J. N. Norris, and H. Ruiz.

Acrochaetium is a notoriously difficult genus, with numerous changing generic concepts resulting in correct species determinations being difficult. There are currently 164 taxonomically recognized species of *Acrochaetium*; 4 of these are known from Puerto Rico.

Comments: Morphological similarities between *Acrochaetium* and *Colaconema* can sometimes make generic separation difficult, and microscopic examination is necessary. These genera primary differ in their size, shape, and number of plastids and pyrenoids. Cells of *Acrochaetium* have stellate plastids and only one pyrenoid, whereas the cells of *Colaconema* have only a single parietal plastid and one pyrenoid. Microscopic examination is best done with fresh living specimens since liquid preservation is known to affect the size and shape of cell organelles. Analyses by Harper and Saunders (2002) revealed *Acrochaetium* and *Colaconema* have distinct genetic lineages.

KEY TO THE *ACROCHAETIUM* SPECIES OF PUERTO RICO

1. Algae growing completely repent . . . . . ***A. repens***
   Algae primarily growing erect 2
2. Algae growing partially as an endophyte in *Liagora* species . . . . . ***A liagorae***
   Algae growing completely external to the host 3
3. Monosporangia in long rows on axes, 10 µm long . . . . . ***A. sanctae-thomae***
   Monosporangia borne, 1–2, on small second branchlets, 14–16 µm long . . . . . ***A. flexuosum***

Acrochaetium flexuosum Vickers

Acrochaetium flexuosum Vickers 1905: 60.
Puerto Rican Records: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.
Western Atlantic Distribution: United States (Massachusetts, Rhode Island, New Jersey, Verginia), Bermuda, Barbados, Cuba, Hispaniola, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Barbados.

Thalli possess a base of creeping filaments that give rise to erect filaments, up to 0.7 mm tall. Branching is alternate and fastigiate. Basal filaments randomly attach at points of contact with the host. Filament cells measure 9.0–10 diam. and 18–35 µm long proximally. Distally the cells are 6.0–7.0 µm diam. and 30–35 µm long. Monosporangia, ovate-oblong, measuring 9.0–10 µm diam. and 14–16 µm long, are usually secundly positioned adaxially on small branchlets.

Habitat and Comments: *Acrochaetium flexuosum* typically occurs epiphytically. [Illustrations: Børgesen 1916: figs. 29, 30.]

Acrochaetium liagorae Børgesen

Acrochaetium liagorae Børgesen 1915: 57–58, figs. 60–62.
Puerto Rican Records: Díaz-Piferrer 1970; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.
Western Atlantic Distribution: United States (Florida), Bermuda, Barbados, Cuba, Hispaniola, Puerto Rico, U.S. Virgin Islands, Brazil, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: St. Croix, U.S. Virgin Islands.

Thalli consist of endophytic prostrate axes growing within the host and erect sparingly and irregularly branched filaments, less than 1.0 mm in length, that sometimes bear terminal hyaline hairs. Filament cells are irregular and cylindrical to cask-shaped and 6.0–14 µm diam. and up to 35 µm long. Cells of erect filaments are longer, up to 400 µm long. Sporangia measure 14 µm diam. and 15–20 µm long and are borne solitarily or in pairs on 1-cell pedicels.

Habitat and Comments: *Acrochaetium liagorae* grows endophytically within various Liagoraceae species. [Illustrations: Aziz 1966: fig. 1a,c; Woelkerling and Womersley 1994, fig. 16; Nunes and Guimarães 2008: figs. 7, 8.]

Acrochaetium repens Børgesen

FIGURE 34
Acrochaetium repens Børgesen 1915: 52, figs. 55, 56.
Puerto Rican Records: Ballantine et al. 2011.
Western Atlantic Distribution: Puerto Rico, U.S. Virgin Islands.
World Distribution: See Guiry and Guiry 2024.
Type Locality: St. Thomas, U.S. Virgin Islands.

Thalli possess endophytic basal filaments that creep below the surface cells of the host in a reticulate pattern or may sometimes be epizootic. The basal filaments are irregularly branched, consisting of barrel-shaped or more irregularly shaped cells. The basal filaments occasionally produce erect filaments above the host alga that are up to 500 µm tall. Cells of the erect filaments measure 7.0–8.0 µm diam. and 24 µm long, and the filaments are terminated by hairlike extensions. Branching is irregular, secund, or rarely opposite. Pedicellate sporangia, 8.0 µm diam. and 14 µm long, are situated at the bases of branches.

Habitat and Comments: *Acrochaetium repens* is known in Puerto Rico from a single epizootic specimen growing on *Anilocra* sp., an isopod fish parasite. The specimen was entirely prostrate and lacking erect sporangia-bearing filaments.

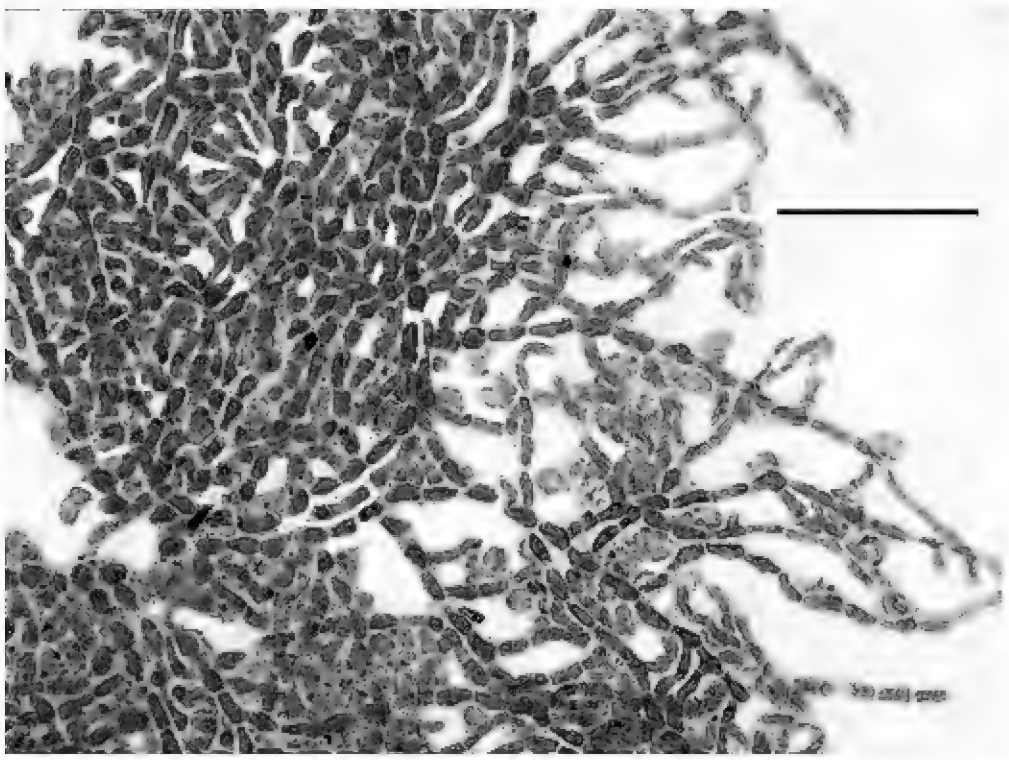

FIGURE 34. *Acrochaetium repens*. DLB0704, growing epizootically on the isopod *Anilocra*. Scale bar = 100 µm.

Acrochaetium sanctae-thomae Børgesen

Acrochaetium sanctae-thomae Børgesen 1915: 30, figs. 23–24.

Puerto Rican Records: Almodóvar and Blomquist 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, Puerto Rico, U.S. Virgin Islands.

World Distribution: See Guiry and Guiry 2024.

Type Locality: St. Thomas Harbor, U.S. Virgin Islands.

Thalli are short statured, reaching to only 0.2–0.3 mm tall, from a unistratose basal disk of more or less confluent filaments. The erect filaments are terminated by elongate hyaline deciduous hairs. Axes are simple or with 1–2 branches. Proximal cells measure 8.0–9.0 µm diam. and 16–18 µm long. Monosporangia, 7.0 µm diam. and 10 µm long, are generally sessile (although sometimes pedicellate) and situated in uniseriate rows on axes and branches.

Habitat and Comments: *Acrochaetium sanctae-thomae* is known from Puerto Rico as an epiphyte of shallow-water species.

Excluded Taxon

***Acrochaetium secundatum* (Lyngb.) Nägeli in Nägeli and Cramer 1858: 532.**

Homotypic Synonym: Chantransia secundata (Lyngb.) Thur. (in Le Jolis 1863: 106).

Acrochaetium secundatum has not been collected in Puerto Rico since the report by Hauck (1888, as *Chantransia secundata*), and we regard the record as unlikely. Woelkerling (1973) reported the species as *Colaconema secundata* (Lyngbye) Woelk., as an epiphyte in the Sargasso Sea.

Colaconematales J.T.Harper et G.W.Saunders

Colaconemataceae J.T.Harper et G.W.Saunders

Colaconema Batters

Colaconema Batters, 1896: 8.

Thalli consist of uniseriate filaments, frequently occurring as epiphytes or being endophytic in varying degrees. Filaments of erect species are normally less than 10 mm high, and cells are generally less than 18 µm diam. Branching of erect axes is irregular, secund, or opposite. Cells generally possess a single parietal plastid with a single pyrenoid. Life histories involve an alternation of isomorphic or slightly heteromorphic generations. Where known, gametophytes are monoecious or dioecious with a fertilized carpogonium giving rise directly to the carposporophyte. Cruciately divided tetrasporangia are borne laterally or terminally on axes and laterals and occur singly or in clusters. Reproduction by monosporangia is the only known reproduction for some species. Fifty species of *Colaconema* are recognized; two of these are known from Puerto Rico.

KEY TO THE *COLACONEMA* SPECIES OF PUERTO RICO

1. Basal endophytic layer is filamentous . . . . . ***C. hypneae***
   Entire thallus within the assimilatory filaments of *Dudresnaya* spp.; the original germinating spore is readily discernible . . . . . ***C. ophioglossum***

Colaconema hypneae (Børgesen) A.A.Santos et C.W.N.Moura

Colaconema hypneae (Børgesen) A.A.Santos et C.W.N.Moura 2010: S74.

Basionym: Chantransia hypneae Børgesen 1909: 2, fig. 2.

Homotypic Synonym: Acrochaetium hypneae (Børgesen) Børgesen 1915: 51, figs. 53, 54.

Heterotypic Synonym: *Acrochaetium seriatum* Børgesen 1915: 32, figs. 25–28.

Puerto Rican Records: As *Acrochaetium hypneae:* Almodóvar et al. 1979; Ballantine and Aponte 1997a, 2002a. As *Acrochaetium seriatum*: Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987.

Western Atlantic Distribution: Caribbean Mexico, Costa Rica, Belize, United States (North Carolina, South Carolina, Georgia, Florida), Bermuda, Cuba, Puerto Rico, U.S. Virgin Islands, Colombia, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2024.
Type Locality: St. Thomas, U.S. Virgin Islands.

Thalli are endophytes with short horizontal basal filaments creeping within the cell wall of the algal host (basiphyte). Cells of the basal filament are short, only slightly longer than broad, and these give rise to erect filaments. Branching of the erect filaments is limited, with the distal branching being secund. Cells of the erect filaments are 7.0–10 µm diam. and 2–3 diameters long. Distal cells measure 6.0–7.0 µm diam. and 3–4 diameters long. Sessile, or rarely pedicellate, monosporangia, 7.0–9.0 µm diam. and 10–12 µm long, are borne adaxially seriate on upper sides of branches.

Habitat and Comments: *Colaconema hypneae* (as *Acrochaetium seriatum*) has been collected as an epiphyte at the algal plains off the south coast of Puerto Rico. [Illustration: Santos and Moura 2010: fig. 1.]

Colaconema ophioglossum (C.W.Schneid.) Alfonso-Carr., M.Sansón et Sangil

Colaconema ophioglossum (C.W.Schneid.) Afonso-Carr., M.Sansón et Sangil 2003: 109, figs. 1–11.
Basionym: Audouinella ophioglossa C.W.Schneid. 1983: 13, 14, fig. 3a–p.
Homotypic Synonym: Acrochaetium ophioglossum (C.W.Schneid.) D.L.Ballant. et N.Aponte 1997a: 151.
Puerto Rican Records: As *Audouinella ophioglossa*: Ballantine and Wynne 1986; Ballantine and Aponte 1997a. As *Acrochaetium ophioglossum*: Ballantine and Aponte 2002a.
Western Atlantic Distribution: United States (North Carolina, Georgia, Florida), Puerto Rico, Brazil.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Onslow Bay, North Carolina, USA.

Thalli consist of erect uniseriate filaments that reach 1.0–3.0 mm tall. The original spore, 8.0–13 µm diam., is persistent and gives rise to 1 or 2 erect axes. Branching is irregular, and axes bear terminal or lateral unicellular hairs. Proximal filament cells measure 4.0–5.0 µm diam. and 45–55 µm long. Ovoid monosporangia, 6.0–13 µm diam. and 13–20 µm long, are borne terminally or laterally on short branchlets. They are either sessile or borne on short stalks. Gametophytes are monoecious. Spermatangia occur on single-celled pedicels and are ~2.5 µm diam. Spherical carposporangia are terminal and measure 10–15 µm diam.

Habitat and Comments: In Puerto Rico, *Colaconema ophioglossum* lives endophytically in *Dudresnaya crassa* at intermediate depths. The axial filaments are not obvious in living specimens because they are roughly the same size and pigmentation as assimilatory filaments of the host. The original spore is readily discernible. [Illustrations: Schneider 1983: fig. 3a–p; Ballantine and Wynne 1986: figs. 2, 3.]

NEMALIALES F.SCHMITZ

GALAXAURACEAE P.G.PARKINSON

Dichotomaria Lam.

Dichotomaria Lam. 1816.

Thalli are lightly to moderately calcified. Algae have terete or flattened axes that are subdichotomously branched. Structurally, thalli possess a filamentous medulla and a pseudoparenchymatous inner cortex that bears multicellular pigmented hairs. Life histories involve an alternation of superficially isomorphic generations; tetrasporophytes and gametophytes differ in cortical cell layer features (Howe 1918b). Spermatangia occur in cavities. Carpogonial branches are 3-celled, and following fertilization, the basal cells produce involucral filaments that give rise to a pericarp. Tetrasporangia are cruciately divided and are borne by stalk cells that form from cortical or subcortical cells.

Comments: Wang et al. (2005) resurrected *Dichotomaria* and provided a detailed account of the genus. Twenty *Dichotomaria* species are recognized, of these there two are known in Puerto Rico.

KEY TO THE *DICHOTOMARIA* SPECIES OF PUERTO RICO

1. Thalli flattened, 1.0–2.5 mm broad ..... ***D. marginata***
   Thalli terete, 1.5–4.0 mm diam. ..... ***D. obtusata***

Dichotomaria marginata (J.Ellis et Sol.) Lam.

FIGURE 35
Dichotomaria marginata (J.Ellis et Sol.) Lam. 1816: 146.
Basionym: Corallina marginata J.Ellis et Sol. 1786: 115, pl. 22: fig. 6.
Homotypic Synonym: Galaxaura marginata (J.Ellis et Sol.) J.V.Lamour. 1816: 264.
Puerto Rican Records: As *Dichotomaria marginata*: Schneider et al. 2016; Ballantine et al. 2016b. As *Galaxaura marginata*: Almodóvar and Blomquist 1961; Almodóvar 1964a, 1964b; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.
Western Atlantic Distribution: Panama, Costa Rica, Caribbean Mexico, United States (Florida), Bahamas, Belize, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Bahamas.

FIGURE 35. *Dichotomaria marginata*. In situ habit photograph, San Cristobal Reef, La Parguera, 8.0 m. Field is approximately 25 cm.

Dichotomaria marginata is the lectotype species of the genus. Thalli measure from 5.0 to 14(–20) cm tall. The smooth branches are flattened, 300–500 µm thick and 1.0–2.5(–5.0) mm broad, and may be transversely banded. The inner cortex of tetrasporophytes possess 2–3 cell layers of pseudoparenchymatous, large, nearly colorless cells with an outer cortex of large, oval to obovoid, sometimes apiculate assimilatory cells, 22–35 µm diam. and 38–50 µm long. In gametophytic thalli, the subcortex is 1–2 cell layers that support the single layer of oval-shaped assimilatory cells, 10–16 µm diam. and 25–40 µm long that form a continuous epidermis. Spherical cystocarps measure 500–600 µm diam. Cruciately divided tetrasporangia are spherical to ovoid and measure 30–45 µm diam. and 35–55 µm long. Algae are rose red in color.

Habitat and Comments: *Dichotomaria marginata* has been collected in a variety of habitats from shallow to deep water in Puerto Rico. *Dichotomaria marginata* was shown to differ molecularly, but only slightly anatomically, from *D. huismanii* C.W.Schneid., Popolizio et Spagnuolo (2016) collected in Bermuda. In their molecular analysis, sequenced specimens from Puerto Rico aligned with other Caribbean *D. marginata* (Schneider et al. 2016). [Additional illustrations: Taylor 1960: pl. 45: figs. 7, 8; Huisman and Borowitzka 1990: figs. 14–27; Littler and Littler 2000: 59; Schneider et al. 2015: figs. 3–6.]

Dichotomaria obtusata (J.Ellis et Sol.) Lam.

FIGURE 36

Dichotomaria obtusata (J.Ellis et Sol.) Lam. 1816: 145.

Basionym: *Corallina obtusata* J.Ellis et Sol. 1786: 113, pl. 22: fig. 2.

Homotypic Synonym: Galaxaura obtusata (J.Ellis et Sol.) J.V.Lamour. 1816: 262.

FIGURE 36. *Dichotomaria obtusata*. DLB4597, Islote, Arecibo, 18 m. Scale bar = 2.0.

Puerto Rican Records: As *Galaxaura obtusata*: Taylor 1960; Ballantine and Aponte 1997a, 2002a; Ballantine et al. 2016b.

Western Atlantic Distribution: Belize, United States (North Carolina, Florida), Bermuda, Bahamas, Barbados, Cuba, Hispaniola, Jamaica, Puerto Rico, Trinidad and Tobago, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Syntype localities: Bahama Islands, West Indies (Huisman and Womersley 1994).

Lectotype: Illustration of Ellis and Solander 1786: pl. 22: fig. 2, selected by Papenfuss et al. 1982.

Highly branched thalli are bushy in appearance. Thalli reach 7.0–10 cm tall, possess a smooth surface, and are lightly calcified. Terete axes are dichotomously branched with jointed segments measuring 1.5–4.0 mm diam. and 7.0–19 mm long. The cortex of tetrasporophytes consists of a single layer of enlarged cells and a middle layer of smaller pigmented cells that each support 1–2 stalked assimilatory cells. These are laterally coherent and are polyhedral in surface view, measuring 27–45 µm diam. Medullary filaments are 10–20 µm diam. The cortex of gametophytes consists of 2 layers of large cells that bear a single outer layer of pigmented cells, 20–30 µm diam. Mature cystocarps, 300–600 µm diam., are immersed and produce carposporangia, 25–35 µm diam. and 30–35 µm long. Cruciately divided tetrasporangia measure 25–35 µm diam. and 30–35 µm long. Algae are pink to red in color.

Habitat and Comments: *Dichotomaria obtusata* is found from very shallow, sheltered habitats down to 59 m depths.

[Additional illustrations: Huisman and Borowitzka 1990: figs. 28–39; Littler and Littler 2000: 61; Huisman 2006: pl. 7; Cormaci et al. 2017: FP143, figs. 1–5.]

Galaxaura J.V.Lamour.

Galaxaura J.V.Lamour. 1812: 185.

Lightly or moderately calcified thalli are erect and pseudodichotomously branched with terete to flattened axes. Branch surfaces are smooth or possess a pigmented filamentous outer cortex. Thalli all have a filamentous medulla. The cortex of gametophytic thalli consists of 3 layers, with a 2-layered inner cortex of large colorless cells that gives rise to an outer cortex of small pigmented cells. Anatomically, tetrasporophytic thalli possess a cortex of either filaments with or without inflated basal cells or an inner 1–3 layers of enlarged colorless cells that bear filaments of smaller pigmented cells. *Galaxaura* displays a life history with an alternation of superficially isomorphic generations; species are either monoecious or dioecious. Spermatangia are formed in subcortical cavities. Female gametophytes possess 3-celled carpogonial branches and carposporangia are formed in a terminal position on gonimoblast filaments. Cruciately divided tetrasporangia are situated laterally or terminally on assimilatory filaments. There are two *Galaxaura* species in Puerto Rico; 25 species are known worldwide. A number of previously recognized *Galaxaura* species reported from Puerto Rico have been synonymized with *Galaxaura rugosa*.

KEY TO THE *GALAXAURA* SPECIES OF PUERTO RICO

1. Axes are densely covered with assimilators throughout . . . . . ***G. comans***
   Branches possess assimilators that are verticillately arranged or do not completely cover axes. . . . . ***G. rugosa***

Galaxaura comans Kjellm.

Galaxaura comans Kjellm. 1900: 44, pl. 2: figs. 10–18, pl. 20: fig. 13.

Puerto Rican Records: Taylor 1960; Ballantine and Aponte 2002a.

Western Atlantic Distribution: Belize, Bahamas, Cuba, Guadeloupe, Jamaica, Puerto Rico, Turks and Caicos, U.S. Virgin Islands, Brazil, Netherlands Antilles.

Type Locality: Guadeloupe.

Thalli reach 12 cm in height and are 3.0–5.0 mm diam. (including assimilators). Crowded branching is alternate, rarely dichotomous, or irregular with internodes reaching 3.0 cm long. Axes are densely covered with assimilators, giving algae a fuzzy appearance. In section, the cortex consists of loosely situated polyhedral cells that each bear a single (rarely 2) assimilatory filament. The medulla consists of filaments 8.0–25 µm diam. and 2 diameters long. Assimilatory filaments basally possess a large oval cell, 50 µm diam. and 80 µm long, becoming cylindrical, with cells measuring ~19 µm diam. Algae lack calcification and are purple red in color.

Habitat and Comments: *Galaxaura comans* is found on rock and coral fragments as well as mangrove prop roots at depths ranging to 12 m. Papenfuss et al. (1982) and Huisman and Borowitzka (1990) considered that *G. comans* was synonymous with *Galaxaura rugosa*. Littler and Littler (2000), Wynne (2017), and Guiry and Guiry (2024) maintain the two species as separate. [Illustrations: Børgesen 1916: figs. 95, 96; Littler and Littler 2000: 59.]

Galaxaura rugosa (J.Ellis et Sol.) J.V.Lamour.

FIGURE 37

Galaxaura rugosa (J.Ellis et Sol.) J.V.Lamour. 1816: 263.

Basionym: *Corallina rugosa* J.Ellis et Sol. 1786: 115, pl. 22: fig. 3.

Heterotypic Synonyms: Galaxaura flagelliformis Kjellm. 1900: 47, pl. 3: figs. 2–11, pl. 20: fig. 16; *G. lapidescens* (J.Ellis et Sol.) J.V.Lamour. 1816: 264; *Galaxaura squalida* Kjellm. 1900: 55, pl. 6: figs. 1–12, pl. 20: fig. 9; *Galaxaura subverticillata* Kjellm. 1900: 48, pl. 3: figs. 12–14, pl. 20: fig. 17.

Puerto Rican Records: As *Galaxaura rugosa*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a; Ballantine et al. 2016b. As *Galaxaura flagelliformis*: Taylor 1960; Almodóvar and Ballantine 1983. As *Galaxaura lapidescens*: Almodóvar and Blomquist 1959; Almodóvar 1962, 1964b; Taylor 1969; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983. As *Galaxaura squalida*: Almodóvar and Ballantine 1983. As *Galaxaura subverticillata*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 2002a.

Western Atlantic Distribution: Belize, Caribbean Mexico, United States (Florida), Bermuda, Bahamas, Costa Rica, Cuba,

FIGURE 37. *Galaxaura rugosa*. DLB5446, Guayacan Island, La Parguera, epiphytic on *Rhizophora* prop root, 1.0 m. Scale bar = 2.0 cm.

Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Eustatius, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Netherlands Antilles, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Jamaica.

Galaxaura rugosa is the lectotype species of the genus. Thalli are bushy, 5.0–12 cm tall and widely dichotomously or alternately branched. The terete branches measure 1.0–3.0 mm diam., and the segments are 2.0–10 mm long. The branch surfaces are either smooth or densely covered with assimilatory filaments. The filaments may be arranged in narrow bands providing the branch with an annulate appearance. Calcification is light and superficial or lacking. The tetrasporophytic thallus inner cortex consists of files of 3 inflated cells, 30–55 µm diam. at the base and decreasing in diameter distally. The outer cortex consists of long or long and short pigmented filaments, to 10–18 µm diam. and to 1.0 mm long. The cortex of gametophytic thalli is pseudoparenchymatous with 3–4 layers of cells that decrease in diameter distally. The innermost and largest of the cortical cells measures 30–60 µm diam. The surface cells, polyhedral in surface view and 18–32 µm diam., are laterally coherent, forming a smooth outer surface. Spermatangia occur in cavities, 200–320 µm diam., that are located just beneath the thallus surface. Carpogonial branches are 3-celled, and cystocarps are round, measuring 400–900 µm diam., with carposporangia 55–65 µm diam. Cruciately divided ovoid to spherical tetrasporangia are terminally positioned on assimilatory filaments and measure 27–33 µm diam.

Habitat and Comments: Taylor (1960) indicated that *G. rugosa* is a shallow-water alga that had also been collected down to 18 m depths. Although it also occurs in shallower water locally, *G. rugosa* has also been reported to a depth of 70 m by Ballantine et al. (2016b). Littler and Littler (1997) argued that *G. subverticillata* and *G. rugosa* were separate species. However, Huisman and Borowitzka (1990) and, later, Huisman et al. (2004), on the basis of molecular evidence, maintained the species as being conspecific. [Additional illustrations: as *G. squalida*, Taylor 1960: pl. 44: fig. 3, pl. 45: fig. 6; as *G. subverticillata*, Taylor 1960: pl. 44: fig. 6, pl. 45: fig. 9; Huisman and Borowitzka 1990: figs. 1–13; as *Galaxaura rugosa*, Huisman 2006: pl. 6; Cormaci et al. 2017: FP147, figs. 1–5.]

Tricleocarpa Huisman et Borow.

Tricleocarpa Huisman et Borow. 1990: 164.

Tricleocarpa is a segregate genus from *Galaxaura*. The life history of the genus involves a heteromorphic alternation of generations. Dichotomously branched gametophyte thalli are calcified and erect. Anatomically, thalli possess a filamentous medulla that is surrounded by a 3–4-layered cortex. A single layer of enlarged cells gives rise to 2 or more progressively smaller cells toward the surface. The dichotomously branched cortical filaments possess cells that decrease in diameter toward the surface. Gametophytic cortical cells lack lateral fusions. Gametophytes are mono- or dioecious. Spermatangia occur in cavities. Carpogonial branches are 3-celled, the lower cells producing multiple branches that contribute to the pericarp of the immersed cystocarp. Pericarps are initiated by filaments originating from the proximal cells of the carpogonial branches. Development of the gonimoblast is direct, and carposporangia are cut off terminally. Filamentous tetrasporophytes are reduced in size and resemble *Acrochaetium*. The cruciately divided tetrasporangia are cut off laterally or terminally. Six species of *Tricleocarpa* are recognized, of which two species are found in Puerto Rico.

KEY TO THE *TRICLEOCARPA* SPECIES OF PUERTO RICO

1. Branches generally less than 1.0 mm diam. . . . . *T. cylindrica*
   Branches 1–2 mm diam . . . . . *T. fragilis*

Tricleocarpa cylindrica (J.Ellis et Sol.) Huisman et Borow.

FIGURE 38

Tricleocarpa cylindrica (J.Ellis et Sol.) Huisman et Borow. 1990: 164.
Basionym: *Corallina cylindrica* J.Ellis et Sol. 1786: 114, pl. 22: fig. 4.
Homotypic Synonym: Galaxaura cylindrica (J.Ellis et Sol.) J.V.Lamour. 1821: 22, pl. 22: fig. 4.
Puerto Rican Records: As *Tricleocarpa cylindrica*: Ballantine and Aponte 1997a. As *Galaxaura cylindrica*: Hauck 1888; Taylor 1960; Almodóvar 1964a, 1964b; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 2002a.
Western Atlantic Distribution: Panama, Costa Rica, Caribbean Mexico, United States (Florida), Barbados, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil, Colombia Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: West Indies.

Tricleocarpa cylindrica is the type species of the genus. Gametophytic thalli are bushy, dichotomously branched, up to 10 cm or more tall and well calcified in the cortical region. The terete axes and branches, 0.45–0.75(–1.0) mm diam., have a firm and smooth texture. Segments are separated by noncalcified joints and measure 5.0–10 mm long. The medulla consists of filaments, 3.0–15 µm diam., that are mostly oriented lengthwise. The cortex is 2–3 cells thick, with innermost cells 18–24 µm diam. Surface cells are about 8.0 µm tall and 10–15 µm diam. Gametophytes are monoecious. Spermatangia occur in cavities, 250–300 µm diam. Cystocarps measure 200–300 µm diam. Tetrasporophytes, known only from culture, are filamentous with filaments measuring ~25 µm diam.

Habitat and Comments: *Tricleocarpa cylindrica* grows on rocks or coral fragments in protected intertidal and shallow

FIGURE 38. *Tricleocarpa cylindrica*. DLBsn, herbarium specimen, Ballena Bay, Guánica, 1.0 m. Scale bar = 2.0 cm.

environments. The species is quite common at Ballena, Bay Guánica. [Additional illustrations: Huisman and Borowitzka 1990: figs. 40–45, 50–52; Littler and Littler 2000: 65; Huisman 2006: fig. 9A–E; Braune and Guiry 2011: fig. 112.1; Hwang and Kim 2011: fig. 61.]

Tricleocarpa fragilis (L.) Huisman et R.A.Towns.

FIGURE 39

Tricleocarpa fragilis (L.) Huisman et R.A.Towns. 1993:100, fig. 1.

Basionym: *Eschara fragilis* L. 1758: 805.

Heterotypic Synonym: Galaxaura oblongata (J.Ellis et Sol.) J.V.Lamour. 1816: 262.

Puerto Rican Records: As *Tricleocarpa fragilis*: Ballantine and Aponte 1997a, 2002a; Ballantine et al. 2016b. As *Galaxaura oblongata*: Taylor 1960; Almodóvar 1964a.

Western Atlantic Distribution: Belize, Costa Rica, Caribbean Mexico, Panama, North America, Bahamas, Barbados, Cuba, Curaçao, Hispaniola, Martinique, Puerto Rico, Trinidad and Tobago, Turks and Caicos, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Oceano American (Jamaica), fide Huisman and Townsend 1993.

Dichotomously branched thalli are bushy and reach 5.0–12 cm tall. The moderately calcified branches, 1.0–2.0 mm diam., are smooth with jointed segments measuring 4–10 diameters long. Apical-most segments are tapered. Longitudinal medullary filaments, 10–20 µm diam., are dichotomously branched. The cortex is lightly calcified and composed of 3–4 cell layers that are about 70 µm thick. Inner cortical cells are contiguous, 35–60 µm diam., bearing an intermediate cortical layer of spherical to oval cells, 25–40 diam. The contiguous surface cells, ~8.0–17 µm diam., are polygonal in surface view and dorsiventrally compressed. Gametophytes may be either monecious or dioecious. Spermatangia occur in conceptacles, 300–350 µm diam. Immersed cystocarps measure 400–500 µm diam. and terminally form ellipsoid carposporangia, 14–27 µm diam. and 34–50 µm long. Algae are pink to rose red in color.

Habitat and Comments: *Tricleocarpa fragilis* grows on rocks or coral fragments in protected environments. Taylor

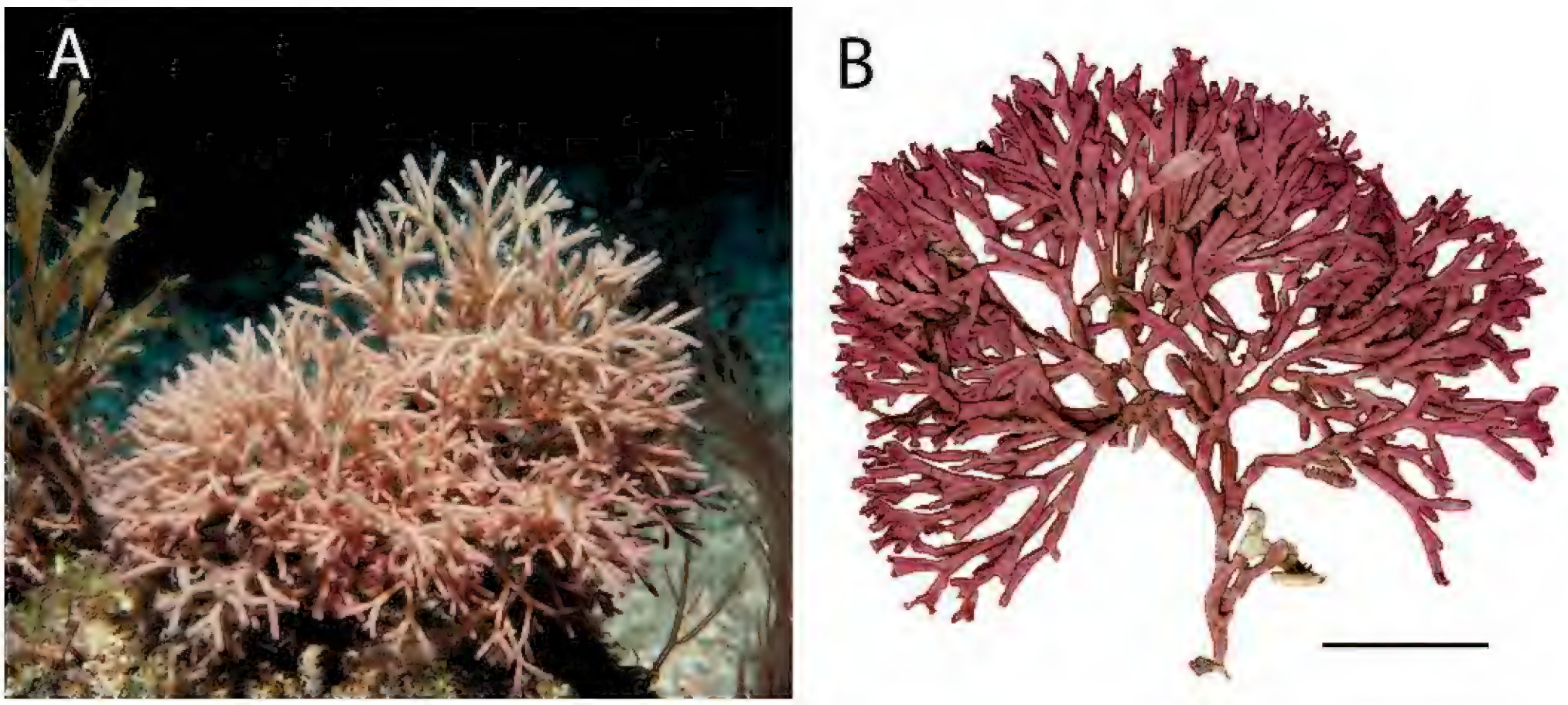

FIGURE 39. *Tricleocarpa fragilis*. (A) In situ habit photograph, 1.5 km seaward Media Luna Reef, 17 m. Field is approximately 8.0 cm. (B) DLB8253, herbarium specimen, Ballena Bay, Guánica, intertidal. Scale bar = 1.0 cm.

(1960, as *Galaxaura oblongata*) also indicated that *T. fragilis* is a shallow-water alga; however, Ballantine et al. (2016b) reported collections of the species down to 70 m depth in Puerto Rico. [Additional illustrations: Huisman and Borowitzka 1990: figs. 46–49, 53–56; Littler and Littler 2000: 67; Cormaci et al. 2017: FP151, figs. 1–3.]

Liagoraceae Kütz.

Ganonema K.C.Fan et Yung C.Wang

Ganonema K.C.Fan et Yung C.Wang 1974: 492.

Calcified or noncalcified thalli are erect and branched dichotomously or irregularly, frequently with short lateral branches. Thalli are mostly soft and highly mucous; some species possess a chalky appearance. Multiaxial axes are terete, possessing a central core of medullary filaments that bear lateral assimilatory filaments. The assimilatory filaments are generally dichotomously branched. Cells of the assimilatory filaments, originating from a swollen basal cell, are cylindrical or ovoid in shape. Basally directed adventitious rhizoidal filaments are frequently produced from proximal cells of the assimilatory filaments and contribute to the medulla. Gametophytic thalli are monoecious or dioecious. Spermatangia are found in dense clusters. Straight to slightly curved carpogonial branches are 3–6 cells in length and borne laterally on proximal cells of assimilatory filaments. Following direct development of the fertilized carpogonium, carposporangia are produced terminally on gonimoblast filaments and may occasionally be quadripartite. A partial involucre is formed by filaments that originate above and below the support cell. Thirteen species of *Ganonema* are recognized, and four of these are known from Puerto Rico.

KEY TO THE *GANONEMA* SPECIES OF PUERTO RICO

1. Branching mainly dichotomous 2
   Branching mainly alternate. 3
2. Axial filaments to 45 µm diam.; cortical cells are cylindrical; calcification farinaceous. . . . . ***G. farinosum***
   Medullary axial filaments to 100 µm diam.; cortical cells are ovoid; calcification not farinaceous . . . . . ***G. vermiculare***
3. Branching alternate above; medullary filaments 100–200 µm diam; assimilatory filaments 19–20 µm . . . . ***G. megagynum***
   Branching alternate to subopposite; axial medullary filaments to 60 µm diam; assimilatory filaments 17–28 µm diam. . . . . ***G. pinnatum***

Ganonema farinosum (J.V.Lamour.) K.C.Fan et Yung C.Wang

FIGURE 40

Ganonema farinosum (J.V.Lamour.) K.C.Fan et Yung C.Wang 1974: 492 [as '*farinosa*'].

Basionym: *Liagora farinosa* J.V.Lamour. 1816: 240.

Puerto Rican Records: As *Ganonema farinosum*: Ballantine and Aponte 1997a, 2002a, 2002b. As *Liagora farinosa*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Belize, Caribbean Mexico, United States (Florida), Bermuda, Bahamas, Barbados, Cayman Islands, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Suez, Red Sea, Egypt.

Thalli are erect and reach 30 cm in height. Thalli are nonlubricous and possess farinaceous calcification. Branching is unevenly dichotomous and frequently may develop numerous short twiglike branch proliferations. Principal axes measure to 2.0(–2.8) mm diam., decreasing to 1.0 mm near the apices. Axes are multiaxial with a compact medulla composed of 20–30 filaments. When viewed in section, rhizoids closely surround the medullary filaments of older thallus axes. Longitudinally oriented medullary cells mostly measure to 200(–300) µm diam. and are to 1,500 µm in length. Surrounding the medulla and incorporating the inner cells of the cortical fascicles is a ring of calcification that measures to 385 µm in thickness. Outwardly directed cortical fascicles are cut off unilaterally from the distal ends of medullary filaments. Initially, the basal cells of the cortical fascicles are little differentiated; however, with distance from the apex, the basal cells become enlarged, 35–45 × 75–90 µm diam. Lower cells of the cortical fascicles cut off rhizoids, 3.0–7.0 µm diam., that are directed inwardly toward the medulla. Cells of the assimilatory filaments are cylindrical, measuring ~14 µm diam. Gametophytes are dioecious. Spermatangia branch initials are cut off from the ultimate 3 or 4 distal cells of the cortical filaments, forming spermatangia 2(–2.5) µm diam. and 3.5(–4) µm long. The entire spermatangial masses appear as dense heads, reaching up to 70 µm diam. Carpogonial branches are almost always 4 cells in length. Cystocarps are compact and hemispherical and measure to 220 µm. The carposporangia are sausage-shaped (botuliform) and measure to 40 µm long. Algae are wine red in color.

Habitat and Comments: *Ganonema farinosum* occurs either solitarily or in dense stands, attached to coral rubble and limestone. The species is seasonally very abundant in the shallow lee of Media Luna Reef, La Parguera. [Additional illustrations: Littler and Littler 2000: 51; Huisman 2006: pl. 10; Cormaci et al. 2017: FP151, figs. 4–6.]

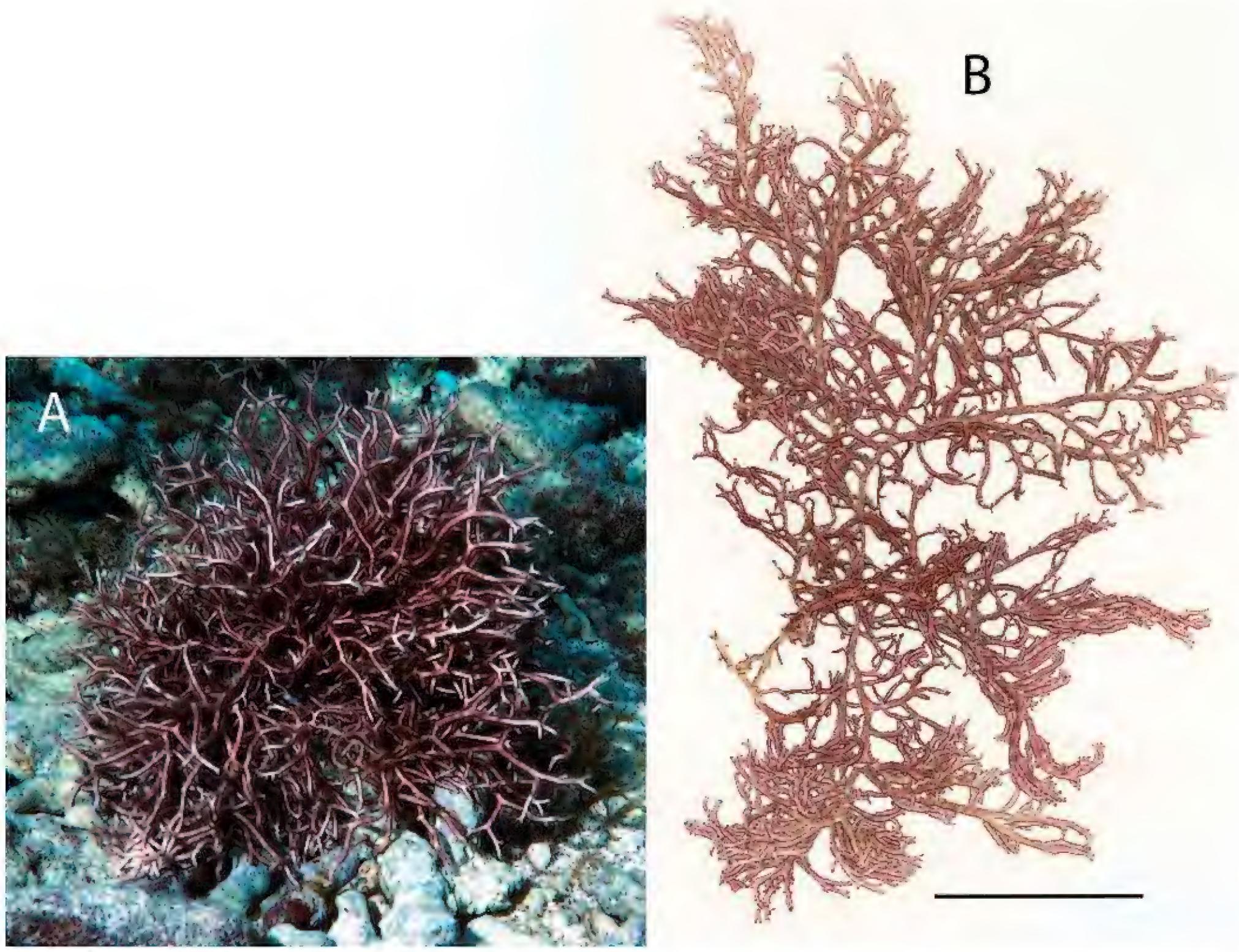

FIGURE 40. *Ganonema farinosum*. (A) In situ habit photograph, leeward Media Luna Reef, 1.0 m. Field is approximately 12 cm. (B) DLB5307, herbarium specimen, Leeward Media Luna Reef, 1.0. Scale bar = 5.0 cm.

Ganonema megagynum (Børgesen) Huisman

Ganonema megagynum (Børgesen) Huisman 2002: 836.

Basionym: Liagora megagyna Børgesen 1915: 77, figs. 82–86.

Puerto Rican Records: As *Liagora megagyna*: Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, Hispaniola, Puerto Rico, U.S. Virgin Islands.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Long Point, St. Croix, U.S. Virgin Islands.

Moderately calcified, highly gelatinous thalli reach 12–14 cm in height and display irregular or dichotomous branching, becoming alternate distally. Axes also possess short lateral branches. Branches are to 1.1 mm diam. Structurally, algae possess a central axis of large, 100–200 µm diam., filaments intermixed with smaller ones, ~11 µm diam. Assimilatory filaments are di-trichotomously branched. These gradually increase in diameter distally, where the cells are oval in shape and measure 19–20 µm diam. and 30–35 µm long. Proximal assimilatory filaments commonly produce rhizoidal filaments. Spermatangia are borne in clusters, 25–50 µm diam. at the apices of assimilatory filaments. Carpogonial branches are 3–5-celled, 20–27 µm diam. Cystocarps with basal involucres measure 150–200 µm diam. and are borne terminally on assimilatory filaments. Algae are pinkish white in color.

Habitat and Comments: *Ganonema megagynum* is known from shallow-water and moderate-depth environments, growing on rocks. [Illustration: Littler and Littler 2000: 53.]

Ganonema pinnatum (Harv.) Huisman

FIGURE 41

Ganonema pinnatum (Harv.) Huisman 2002: 828.

Basionym: *Liagora pinnata* Harv. 1853: 138, pl. 31B.

Puerto Rican Records: As *Liagora pinnata*: Díaz-Piferrer 1963; Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Belize, Caribbean Mexico, United States (Florida), Bahamas, Cuba, Hispaniola, Jamaica, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Sand Key, Florida, USA.

Moderately calcified thalli reach 11 cm in height, and axes are 1.5 mm diam., decreasing to 0.5 mm diam. distally. Branching overall is complanate with abundant short lateral branches. Algae are soft in texture but not abundantly lubricous. Central axial filaments measure to 60 µm diam. proximally, decreasing to about 15 µm diam. distally. Assimilatory filaments, cut off by axial cells, are dichotomously branched and comprised of subcylindrical to slightly swollen cells that increase in diameter, to 17–28 µm, distally. Gametophytic thalli are dioecious with spermatangia in tufts, 25–49 µm broad, produced by apical and subapical assimilatory cells. Carpogonial branches are 4(–5)-celled long. Cystocarps possess well-developed involucral filaments. Algae are pale pink to white in color.

Habitat and Comments: Taylor (1960, as *Liagora pinnata*) reported *Ganonema pinnatum* to be an alga of shallow water. In Puerto Rico it also encountered at moderate depths. [Additional illustrations: as *Liagora pinnata*, Abbott 1990: figs. 5, 6; as *Ganonema pinnatum*, Huisman 2006: fig. 17C,D, pl. 13.]

Ganonema vermiculare D.L.Ballant. et I.A.Abbott

FIGURE 42

Ganonema vermiculare D.L.Ballant. et I.A.Abbott 2006: 122–124, figs. 1–13.

Puerto Rican Records: Ballantine and Abbott 2006.

Western Atlantic Distribution: Puerto Rico.

Type Locality: 1.5 km seaward Media Luna Reef, La Parguera, Puerto Rico.

Lubricous thalli reach 23 cm in length with axes measuring 1.3 to 2.0 mm diam. below,decreasing distally to 0.5 mm diam. Branching is dichotomous below, becoming irregular and radially alternate distally. Occasional short adventitious branchlets, 3.0 to 6.0 mm long, may be produced in the upper portions of the algae. The longitudinal medullary filaments are closely compact, to 150 µm diam. Medullary cells typically give rise to single cortical fascicles laterally. The light calcification occurs in a cylinder surrounding the central medullary region. Assimilatory filaments extend 250–300 µm beyond the cylinder. The basal cells of the cortical fascicles in lower portions are either enlarged and isodiametric or elongate and enlarged distally to a maximum diameter of 32 µm. In distal areas, the basal cells are not differentiated. The assimilatory filaments are 3 times di-trichotomous. Frequent colorless glandular hair-tipped cells (or their scars) are found on terminal cells. The cortical fascicles are made up of ovoid cells that are 10–17.5 µm diam. proximally and to 10 µm diam. distally. Lower cells of the cortical fascicles produce abundant rhizoidal filaments that grow back toward the medulla, where they come to lie alongside and intersperse with the longitudinal medullary filaments. Algae are dioecious. Spermatangia are ~2.5 µm diam. and are cut off in abundant dense heads from the distal 2 (or occasionally 3) cells of the assimilatory filaments. Carpogonial

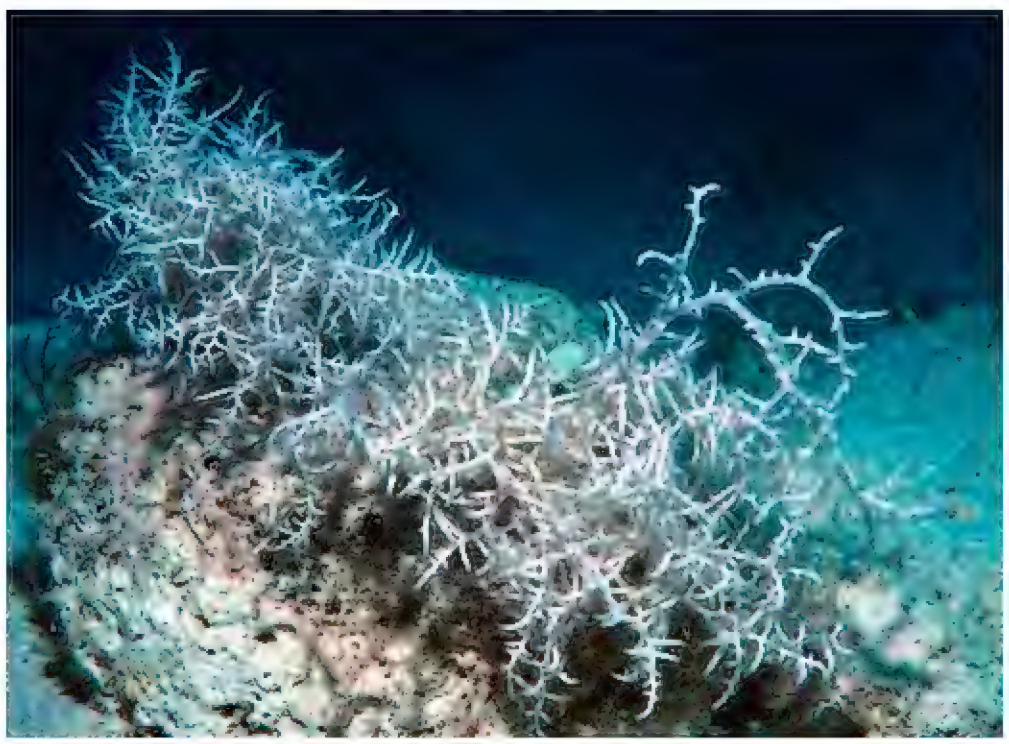

FIGURE 41. *Ganonema pinnatum*. In situ habit photograph, leeward Media Luna Reef, 15 m. Field is approximately 15 cm.

FIGURE 42. *Ganonema vermiculare*. In situ habit photograph, 1.5 km seaward Media Luna Reef, 17 m. Field is approximately 15 cm.

branches are (3–)4(–5)-celled and are typically formed at the upper shoulders or at the distal ends of inner cortical fascicle cells. Following presumed fertilization, branches of the sterile filaments cut off by the support cell proliferate and densely surround the carpogonial branch. Carposporophytes measure 150 to 220 µm diam., with individual carposporangia being pyriform and up to 7.5 µm diam. and 15 µm long.

Habitat and Comments: *Ganonema vermiculare* occurs attached to loose shell or carbonate substrata at the offshore algal plains at depths of 11 to 17 m. The species is endemic, currently known only from the southern Puerto Rican coast.

Gloiocallis S.M.Lin, Huisman et D.L.Ballant.

Gloiocallis S.M.Lin, Huisman et D.L.Ballant. 2014: 48.

Lightly calcified, erect thalli, arising from a discoid holdfast, reach up to 15 cm in height. Thalli have 1 or few main axes with pinnate branches; branching is up to 4 or 5 orders. Cells of assimilatory filaments are cylindrical with or without terminal hairs. Carpogonial branches are 3- or 4-celled and borne on inner cortical cells. The carpogonial branches are encircled by 3 to 4 involucral filaments produced from cortical cells adjacent to the supporting cells; most cells of gonimoblasts differentiate into carposporangia. *Gloiocallis* is a monotypic genus.

Gloiocallis dendroidea (P.Crouan et H.Crouan) S.M.Lin, Huisman et D.L.Ballant.

FIGURE 43

Gloiocallis dendroidea (P.Crouan et H.Crouan) S.M.Lin, Huisman et D.L.Ballant. 2014: 49, figs. 42–47.

Basionym: Helminthora dendroidea P.Crouan et H.Crouan in Mazé and Schramm 1878: 178.

Homotypic Synonyms: *Ganonema dendroideum* (P.Crouan et H.Crouan) D.L.Ballant. et N.Aponte 2002b: 220; *Liagora dendroidea* (P.Crouan et H.Crouan) I.A.Abbott 1990: 317.

Heterotypic Synonym: *Liagora mucosa* M.Howe 1920b: 556–557.

Puerto Rican Records: As *Gloiocallis dendroidea*: Lin et al. 2014. As *Ganonema dendroideum*: Ballantine and Aponte 2002a, 2002b. As *Liagora dendroidea*: Ballantine and Aponte 1997a. As *Liagora mucosa*: Almodóvar and Blomquist 1961; Almodóvar 1964a, 1964b; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Belize, Caribbean Mexico, United States (Florida), Bermuda, Bahamas, Barbados, Cayman Islands, Cuba, Guadeloupe, Hispaniola, Puerto Rico, Brazil, Colombia.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Pointe-a-Pitre, Ilet a Cochons, Guadeloupe Island.

Thalli are lightly calcified and highly lubricous, to 15 cm in height. Cortical fascicles, cut off from the distal ends of axial cells, are issued unilaterally. Medullary cells are colorless and measure to 125 µm in diameter. The assimilatory filaments are moniliform and measure to 18 µm in diameter. Assimilatory cells are 4 to 5 times longer than broad proximally and become isodiametric distally. Basal cells of lateral fascicles are to 20 µm diam. and are elongate, to 5 times longer than broad, in younger algal portions. In older thallus portions they are swollen, to 50 µm diam., and are 2 to 3 times longer than broad. The basal cells of the cortical fascicles cut off 3, rarely 2, cortical branchlets, which are directed outward. They also give rise to downwardly coursing rhizoids that may cut off cortical laterals. Carpogonial branches are located toward the base of the cortical fascicle and are normally cut off singularly, although polycarpogonial branches are known. The carposporophytes are compact, measuring to 200 µm diam., and carposporangia are ovate to pyriform in shape, measuring to 25 µm diam. and to 37 µm long.

FIGURE 43. *Gloiocallis dendroidea*. DLB5787, herbarium specimen, leeward Media Luna Reef, La Parguera, 1.0 m. Scale bar = 1.0 cm.

Habitat and Comments: *Gloiocallis dendroidea* has been collected in shallow back-reef environments of La Parguera. [Additional illustrations: as *Liagora mucosa*, Abbott 1990: figs. 12, 13.]

Helminthocladia J.Agardh

Helminthocladia J.Agardh 1851: 412, 413, nom cons.

Highly lubricous, multiaxial thalli are uncalcified. Thalli are bushy and alternately or radially branched. A loose medulla of longitudinal axial filaments produces assimilatory filaments radially. The assimilatory filaments are broadest distally. Spermatangia occur in laterally placed compact clusters located distally on assimilatory filament cells. Carpogonial branches, borne on inner assimilatory cells, are 3- or 4-celled. Cystocarps

are involucrate, and terminal cells of the gonimoblasts become carposporangia. Tetrasporophytes are filamentous, producing terminal cruciately divided tetrasporangia. There are 20 *Helminthocladia* species recognized worldwide, 1 of which is known from Puerto Rico.

Helminthocladia calvadosii (J.V.Lamour. ex Duby) Setch.

Helminthocladia calvadosii (J.V.Lamour. ex Duby) Setch. in Collins et al. 1915: no. 2035.

Basionym: Dumontia calvadosii J.V.Lamour. ex Duby 1830: 941.

Puerto Rican Records: As *Helminthocladia calvadosii*: Díaz-Piferrer 1970; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Bermuda, Puerto Rico, St. Eustatius, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Calvados, Normandy, France.

Thalli are bushy and very gelatinous, reaching to 20–60 cm tall. Primary axes are terete or compressed, measuring 2.0–15 mm diam. proximally and 0.4–2.0 mm diam. distally. Branches are somewhat thicker in the middle than near the base and greatly tapering to the tips. Branching, to 2–3 orders, is irregular to radial. The medulla is compact, composed of longitudinal axial filaments, to 12 µm diam. and to 160 µm long. Cortical fascicles are cut off from each medullary cell. The assimilatory filaments are short, 4–6 cells and to 180 µm long. Lower cells of the cortical fascicles give rise to descending rhizoids. The assimilatory filaments are terminated by pyriform cells, 20–25 µm diam. Gametophytes are monoecious. Spermatangial clusters are borne on terminal cells of the assimilatory filaments. Carpogonial branches, borne on inner cells of the cortical fascicles, are 2–4-celled. Following fertilization, the loosely arranged gonimoblasts bear ovoid carposporangia, 7.0–9.0 µm diam. and 15–20 µm long, terminally. Algae are dull purple or reddish in color.

Habitat and Comments: Algae are found in shallow protected environments. *Helminthocladia calvadosii* is not common in Puerto Rico, and its presence in Puerto Rico is based on the single report of Díaz-Piferrer (1970). Species assignment of Puerto Rican collections of *Helminthocladia* to *H. calvadosii* should be critically reexamined in light of the Popolizio et al. (2013) description of *Helminthocladia kempii* Popolizio, Schneider, Chengsupanimit, Saunders et Lane. Popolizio et al. (2013) decided that all Bermudan specimens under the name *H. calvadosii* were referrable to their new species. However, one vegetative character separating the Bermudan species from specimens near the type locality of *H. calvadosii* (eastern Atlantic) is subdichotomous branching, seen near the apices, versus irregular to pectinate in the European specimens. On the basis of the rather poor figures (figs. 1–3 of *H. calvadosii* in Díaz-Piferrer 1970: 11), branching would have to be regarded as more pectinate than dichotomous. Unfortunately, we have not been able to locate Díaz-Piferrer's specimens in MSM. [Illustrations: Guimarães et al. 1990: figs. 1–12; O'Dwyer and Afonso-Carrillo 2001: figs. 1–18.]

Helminthora J.Agardh

Helminthora J.Agardh 1851, nom. cons.

Lubricous thalli are calcified or not. Thalli are erect and generally abundantly branched. The terete axes possess a filamentous medulla and a cortex of branched assimilatory filaments. The distal-most assimilatory filament cells are smaller than subtending cells. Carpogonial branches, 3- or 4-celled, are of accessory origin and are borne on inner assimilatory filament cells. Following fertilization, only the upper cell resulting from initial zygote division takes part in gonimoblast initiation. Vegetative cells neighboring the carpogonial branch cut off sterile filaments that surround the developing gonimoblast. Cruciately divided tetrasporangia are cut off by filamentous tetrasporophytes. One of the eight recognized species of *Helminthora* is known from Puerto Rico.

Helminthora anomala S.Vélez et Vega

FIGURE 44

Helminthora anomala S.Vélez et Vega 2005: 836, figs. 1–12.

Puerto Rican Records: Vélez-Villamil and Vega Pagán 2005; Vélez-Villamil 2008.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Luis Peña Key, Culebra, Puerto Rico.

Moderately calcified, highly lubricous thalli reach 6.0–7.0 cm tall. Thalli have terete axes, 1.0–2.0 mm diam., and are dichotomously branched. The medullary filaments measure 25–30 µm diam. and 220–290 µm long. Assimilatory filaments, 280–330 µm long, are dichotomously branched. Proximal cells of the assimilatory filaments are cylindrical, 6.0–7.0 µm diam., and distal cells are ovoid, 10–12 µm diam. Gametophytes are monoecious. Carpogonial branches are 4–5 cells in length and are laterally positioned. Carposporangia, borne singly and terminally, are obovoid to ovoid, 5.0–8.0 µm diam. and 11–13 µm. long. Algae are pinkish gray in color.

Habitat and Comments: The species, growing in tufts, is known only from collections at 3.0–12 m depths at Culebra and "El Natural," Aguadilla, the type locality. Velez-Villamil (2008) demonstrated that the species exhibited a heteromorphic triphasic life history with a reduced sporophytic phase. Microthalli produced both monosporangia and cruciately divided tetrasporangia. Monospores gave rise to further sporophyte thalli. Cruciately divided tetrasporangia released tetraspores that gave rise through heterotrichous growth to gametophytes. New tetrasporocytes continually develop within empty sporangial walls.

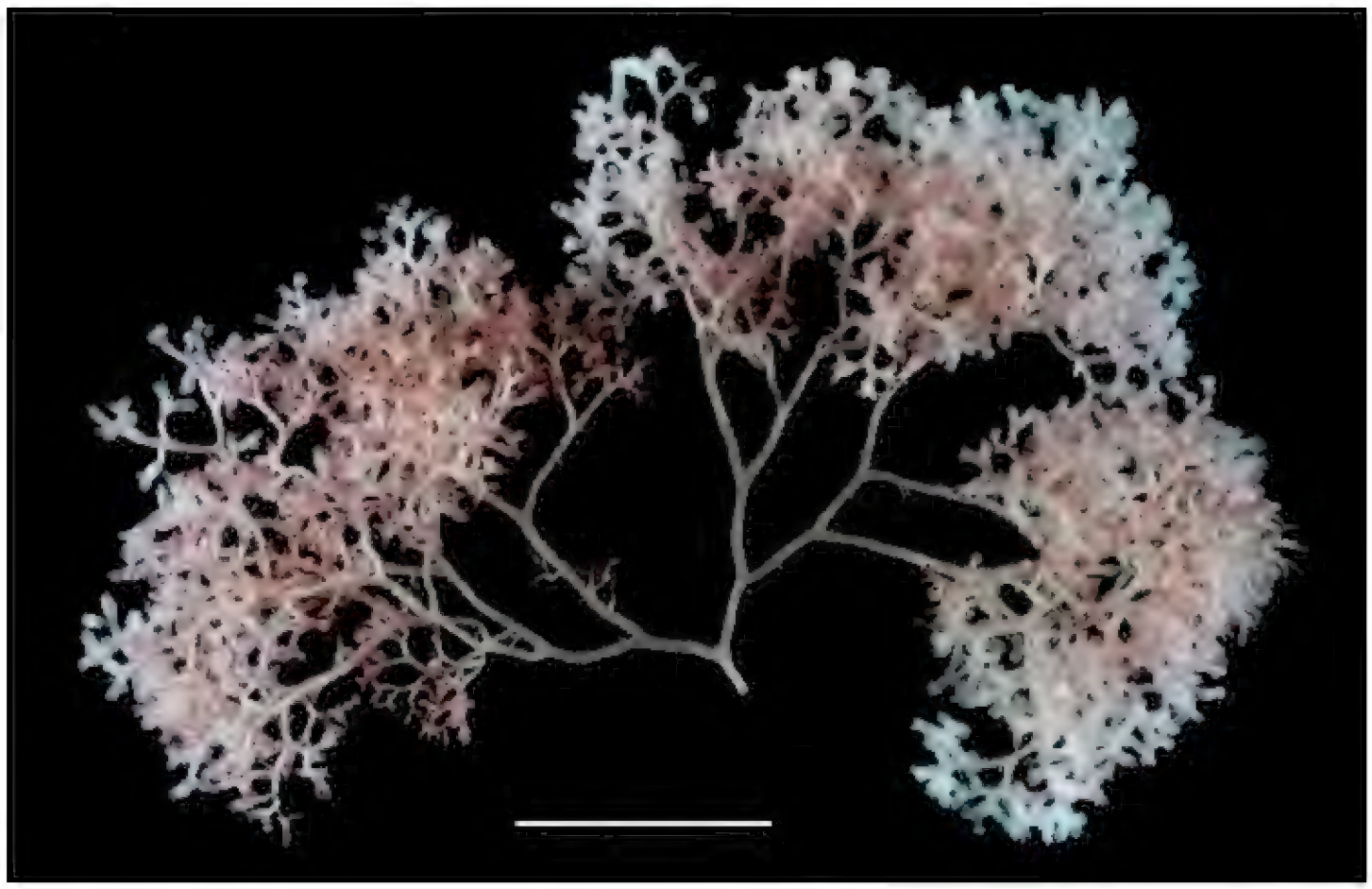

FIGURE 44. *Helminthora anomala*. DLBsn, herbarium specimen, Leeward Media Luna Reef, 6.0 m. Scale bar = 2.0 cm.

Excluded Taxon

***Izziella orientalis* (J.Agardh) Huisman et Schils 2002: 247.**

Basionym: Liagora orientalis J.Agardh 1896: 99.

Liagora orientalis is listed by Ballantine and Aponte (2002a) in the Puerto Rico algal flora, presumably based on a misidentified specimen in MSM. Until the reports by Díaz-Pulido and Diaz (1997) and Díaz-Pulido and Diaz-Ruíz (2003), from Atlantic Colombia, *L. orientalis* was exclusively known from the Pacific. Abbott (1990) discussed the morphological similarity between *L. orientalis* and other *Liagora* species.

Liagora J.V.Lamour.

Liagora J.V.Lamour. 1812: 185.

Erect, lubricous thalli are calcified to various degrees. Algae have terete, dichotomously or irregularly branched axes, frequently possessing numerous short lateral branches. Calcification is firm to light, often giving the thallus a chalky appearance. Structurally, multiaxial thalli possess central longitudinally oriented medullary filaments. These give rise to a cortex of branched assimilatory filaments. Downward-coursing rhizoidal filaments are often cut off by proximal cells of the assimilatory filaments. Distal assimilatory filament cells may possess hairs or glandular cells. Gametophytes are monoecious or dioecious. In male gametophytes, spermatangial parent cells are cut off by distal cortical cells, singly or in clusters. Carpogonial branches, 3–6 cells in length, are cut off from proximal or mid-level assimilatory cells. There is direct development of the carposporophyte from the fertilized carpogonia. Gonimoblasts are diffuse or compact. Carposporangia are borne terminally on gonimoblast filaments and may either be simple or quadripartite. Tetrasporophytes are reduced uncalcified filamentous stages. There are 2 *Liagora* species in Puerto Rico; 55 species are recognized worldwide. A number of *Liagora* species that were previously reported from Puerto Rico have been since assigned to other genera (see, for example, *Ganonema*, *Gloiocallis*, *Titanophycus*, *Trichogloeopsis*).

KEY TO THE *LIAGORA* AND *TITANOPHYCUS* SPECIES OF PUERTO RICO

1. Thalli moderately calcified and flexible 2
   Thalli more heavily calcified and stiff . . . . . *T. validus*
2. Gonimoblast compact . . . . . *L. ceranoides*
   Gonimoblast diffuse . . . . . *L. tsengii*

Liagora ceranoides J.V.Lamour.

FIGURE 45

Liagora ceranoides J.V.Lamour. 1816: 239.

Puerto Rican Records: Taylor 1960; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Belize, Costa Rica, Panama, Caribbean Mexico, United States (Florida), Bermuda, Bahamas, Barbados, Cayman Islands, Costa Rica, Cuba, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: St. Thomas, U.S. Virgin Islands.

Moderately calcified thalli are compact growths, 4.0–8.0 cm diam. The surface texture is soft and proximally, farinaceous. Axes measure 1.0–2.0 mm diam., and branching is dichotomous distally. Cells of the assimilatory filaments measure 20–40 µm diam. and 5 diameters long. The assimilatory filaments, composed of moniliform cells, 6.0–11 µm diam., branch at wide angles and barely extend beyond the calcification in the mucous. Male gametophytes form platelike spermatangial clusters. Spherical cystocarps possess well-developed involucres and measure 100–500 µm diam. Algae are nearly white in color.

Habitat and Comments: The species is common in shallow water and is known to 20 m depth. [Additional illustrations: Huisman 2006: pl. 15; Littler et al. 2008: 33; Braune and Guiry 2011: fig. 114.1; Lin et al. 2013: figs. 19–23.]

FIGURE 45. *Liagora ceranoides*. In situ habit photograph, leeward Media Luna Reef, 15 m. Field is approximately 15 cm.

Liagora tsengii Huisman et M.J.Wynne

FIGURE 46

Liagora tsengii Huisman et M.J.Wynne 1999: 219–220, figs. 1–10.

Puerto Rican Records: Ballantine et al. 2015.

Western Atlantic Distribution: Caribbean Mexico, Cuba, Guadeloupe, Puerto Rico, St. Kitts.

Type Locality: Timothy Beach, St. Kitts, Lesser Antilles.

Thalli are up to 6.0 cm tall and mostly dichotomously branched. Calcification is heavy, and the thallus surface is roughened. Internally, the longitudinally oriented medullary filaments measure 15–35 µm diam., and the assimilatory filaments of the cortical fascicles are 300–450 µm long and mostly dichotomously branched. The proximal, nearly cylindrical assimilatory cells, 5.0–7.0 µm diam., become ovoid distally and increase to 10–12 µm in diam. The outermost assimilatory cells are subspherical and measure 7.0–11 µm diam. Gametophytes are dioecious, with assimilatory filaments of females bearing 5(–6)-celled carpogonial branches, produced from the mid to outer regions of the assimilatory filaments. The carposporophyte is originally compact; however, it becomes less so with maturation. In spermatangial thalli, the apical cell of assimilatory fascicles frequently produces 2 additional cortical cells laterally, which in addition to the subapical cells give rise to spermatangial parent cells that then produce spermatangia that average 2.5 µm diam.

Habitat and Comments: *Liagora tsengii* in Puerto Rico is known only from leeward of Media Luna Reef at 6.0 m depth. Prior to the Puerto Rico report of Ballantine et al. (2015), *Liagora tsengii* had been reported only for the Lesser Antilles from

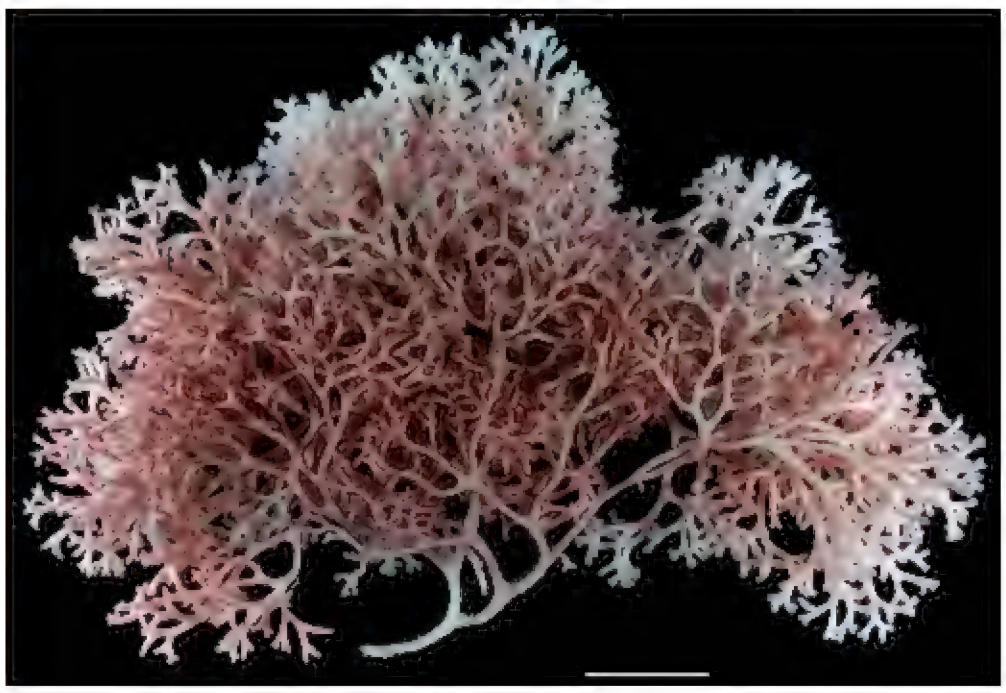

FIGURE 46. *Liagora tsengii*. DLB7217, leeward Media Luna Reef, 1.0 m. Scale bar = 1.0 cm.

St. Kitts (type locality) and Guadeloupe. [Additional illustrations: Ballantine et al. 2015: figs. 1–5.]

Titanophycus Huisman, G.W.Saunders et A.R.Sherwood

Titanophycus Huisman, G.W.Saunders et A.R.Sherwood 2006: 81.

Erect thalli are dichotomously branched with terete axes. Thalli are strongly calcified, frequently appearing chalky. Structurally, thalli possess longitudinally oriented medullary cells that give rise to assimilatory filaments. The assimilatory filaments are sparingly dichotomously branched. Gametophytes are dioecious. Spermatangia occur in dense tufts arising from distal cells of cortical filaments. Carpogonial branches, borne laterally on median-positioned assimilatory filament cells, are 4– or 5-celled. Following fertilization, a fusion cell does not form, and the carpogonial branch cells remain conspicuous during gonimoblast development. A loose involucre of sterile filaments surrounds the developing cystocarp, and gonimolobes cut off carposporangia terminally. Of three known *Titanophycus* species, one is recognized from Puerto Rico.

Titanophycus validus (Harv.) Huisman, G.W.Saunders et A.R.Sherwood

FIGURE 47

Titanophycus validus (Harv.) Huisman, G.W.Saunders et A.R.Sherwood 2006: 119, fig. 34, pl. 17.

Basionym: Liagora valida Harv. 1853: 138, pl. 31A: figs. 1–5.

Heterotypic Synonym: Liagora annulata J.Agardh 1876: 518.

Puerto Rican Records: As *Liagora annulata*: Hauck 1888. As *Liagora valida*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

FIGURE 47. *Titanophycus validus*. In situ habit photograph, leeward Media Luna Reef, 15 m. Field is approximately 6.0 cm.

Western Atlantic Distribution: Belize, Caribbean Mexico, Panama, United States (Florida), Bermuda, Bahamas, Barbados, Cayman Islands, Guadeloupe, Hispaniola, Jamaica, Puerto Rico, St. Eustatius, St. Martin, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Sand Key, Florida, USA.

Titanophycus validus is the type species of the genus. Thalli reach up to 15 cm tall, and the terete dichotomous branches are to 1.5 mm diam., tapering to 0.8 mm diam. Calcification is heavy to the extent that proximal portions may be rigid; however, calcification becomes lighter distally. Medullary filament cells are slightly swollen, 20–40 µm diam. and 10–20 diameters long. Rhizoidal filaments, 5.0–10 µm diam., are also present within the medulla. Assimilatory filaments, to 16 µm diam. and 250 400 µm long, are branched 4–5 times. The distal assimilatory cells are oval to pyriform, 10–15 µm diam. Spermatangial clusters are platelike and borne distally on assimilatory cells. Carpogonial branches are 4–5-celled. Cystocarps, ~400 µm diam., are surrounded by a few involucral filaments of oval cells. Thalli are chalky white in color, sometimes with pinkish apices.

Habitat and Comments: Littler and Littler (2000) report the species in water less than 2.0 m depth. In Puerto Rico the species has commonly been collected at the offshore algal plains. [Additional illustrations: Littler and Littler 2000: 55.]

Trichogloea Kütz.

Trichogloea Kütz. 1847: 53.

Thalli are highly lubricous, with calcification associated with the outer medulla. Branching is alternately radial, and axes are multiaxial. The medulla consists of a loose and calcified central core with longitudinally oriented filaments, 20–45 diam. (or greater), and an outer medulla of rhizoidal filaments. The inner medullary cells give rise to fascicles of assimilatory filaments. The assimilatory filaments comprise cells mostly cylindrical proximally and ellipsoid or moniliform terminally. The cortical cells are largely immersed in a thick mucilaginous layer. Gametophytes are monoecious or dioecious. Spermatangia are clustered terminally or on subterminal cortical cells. Carpogonial branches are 6–9-celled and are situated on the distal or median portion of assimilatory filaments. Involucres are not formed, and the cystocarp is stalked. Most gonimoblast cells form carpospores. Tetrasporophytes are unknown. One of the three recognized *Trichogloea* species is known from Puerto Rico.

Trichogloea requienii (Mont.) Kütz.

FIGURE 48

Trichogloea requienii (Mont.) Kütz. 1847: 54.

Basionym: Batrachospermum requienii Mont. 1843: 355 [Montagne 1843].

Puerto Rican Records: Taylor 1960; Ballantine and Aponte 1997a, 2002a.

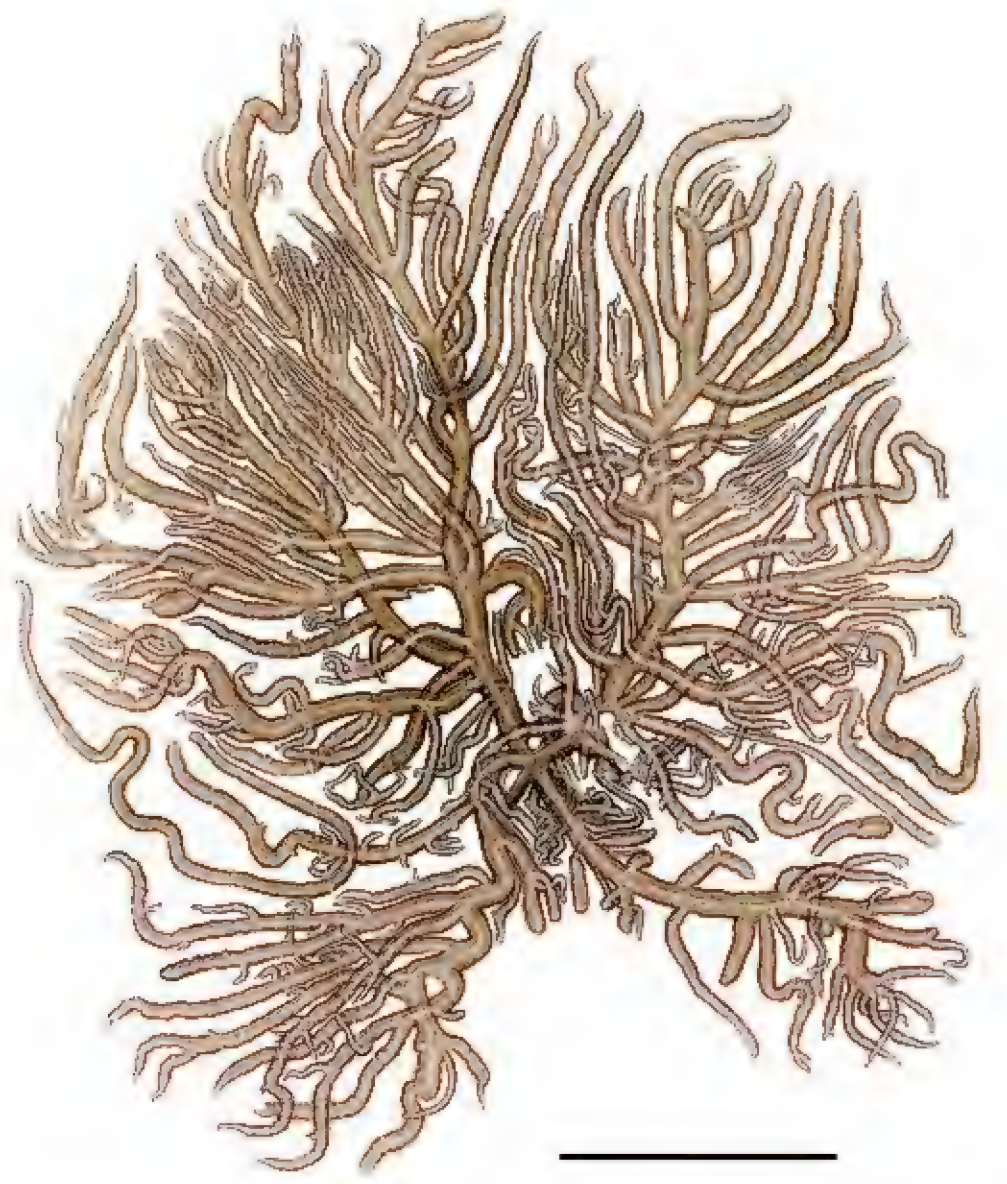

FIGURE 48. *Trichogloea requienii*. DLB5552, herbarium specimen, Flamingo Beach, Culebra Island, <1.0 m. Scale bar = 5.0 cm.

Western Atlantic Distribution: Caribbean Mexico, Barbados, Cuba, Hispaniola, Martinique, Puerto Rico, Brazil, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: "Mari Rubro" [Red Sea].

Trichogloea requienii is the type species of the genus. Thalli reach 25 cm in height. Thalli are bushy and repeatedly branched; principal axes are 2.0–7.0 mm diam., and higher-order branches measure 1.0–2.0 mm diam. The medulla, 1.0–2.0 mm thick, comprises longitudinally oriented filaments, 18–35 µm diam. Assimilatory filaments are embedded in a thick, 0.5–1.0 mm diam., mucous layer. The dichotomously branched assimilatory filaments possess enlarged distal cask-shaped cells, 12–22 µm diam. and 22–28 µm long. Adventitious rhizoids are abundantly produced from proximal assimilatory cells. Gametophytes are dioecious. Spermatangia occur subterminally on cells of the cortical filaments. Carpogonial branches, to 8 or more cells long, are borne terminally on cortical filaments. The lower 3–4 cells of the carpogonial branch give rise to once- or twice-branched involucral filaments. Cystocarps measure 130–150 µm diam. Ovoid carposporangia measure 5.0–9.0 µm diam. and 11–18 µm long. Algae are purplish red in color and white where calcified.

Habitat and Comments: *Trichogloea requienii* was reported by Littler and Littler (2000) as living on hard substrata in water to 15 m deep; the only known Puerto Rican collection was at Culebra Island at a depth of less than 1.0 m deep. [Additional illustrations: Moura et al. 1999: figs. 1–26; Abbott and Huisman 2005: figs. 1–15; Huisman 2006: fig. 36A–C, pl. 20.]

Excluded Taxon

***Trichogloea herveyi* W.R.Taylor 1951: 119–120.**

The species was reported for Puerto Rico by Almodóvar (1965). We have been unable to locate voucher specimens in MSM and believe the report is based on a misidentification of *T. requienii.*

Trichogloeopsis I.A.Abbott et Doty

Trichogloeopsis I.A.Abbott et Doty 1960: 636.

Lubricous thalli, to 30 cm in height, are lightly calcified. A multiaxial medullary core of longitudinally oriented filaments bear assimilatory filaments. Cells of the assimilatory filaments are moniliform distally. Gametophytes are usually dioecious. Spermatangia occur in capitula. Carpogonial branches are 3–6-celled and borne terminally. Cystocarps are not normally surrounded by involucres; however, sterile filaments are cut off by gonimoblast filaments are basally directed and surround the carpogonial branch. Carpospores are produced singly on terminal cells of the gonimoblast. A single species of the six known *Trichogloeopsis* species is known from Puerto Rico.

Trichogloeopsis pedicellata (M.Howe) I.A.Abbott et Doty

FIGURE 49

Trichogloeopsis pedicellata (M.Howe) I.A.Abbott et Doty 1960: 638, figs. 18–20.

Basionym: Liagora pedicellata M.Howe 1920b: 556.

Puerto Rican Records: Vélez-Villamil et al. 2000, Ballantine and Aponte 2002a; Lin et al. 2014.

Western Atlantic Distribution: Belize, Costa Rica, Caribbean Mexico, United States (Florida), Bermuda, Bahamas, Cuba, Hispaniola, Jamaica, Martinique, Puerto Rico, Turks and Caicos, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Cockburn Harbor, South Caicos Island, Turks and Caicos.

Thalli are highly lubricous, flaccid, and moderately calcified, reaching 4.0 to 16 cm tall. Axes measure 1.5–2.5 mm diam. proximally. Branching is irregularly alternate or paniculate, and branches, 1.2–2.5 mm diam. below, become successively shorter in higher branching orders. The medulla is

FIGURE 49. *Trichogloeopsis pedicellata*. DLBsn, live specimen, leeward Media Luna Reef, La Parguera, 1.0 m. Scale bar = 2.0 cm.

composed of longitudinally oriented medullary filaments, 30–100 µm diam., that are intermixed with rhizoidal filaments, 8.0–13 µm diam. Assimilatory filaments are mostly dichotomously branched and distally measure 13–20 µm diam. where cells are moniliform or obovoid. Gametophytes are monoecious. Straight carpogonial branches, 4–6 cells long, are borne on outer assimilatory cells. Carpogonial branches include an elongated basal cell (the pedicel). The compact cystocarp is hemispherical in shape and borne on the elongate, 450 µm long, carpogonial branch. Carpospores are pyriform, 15–21 µm diam. and 23–39 µm long. Algae are pale pink to white in color.

Habitat and Comments: *Trichogloeopsis pedicellata* grows on rocks and coral fragments, frequently in back-reef environments. Velez-Villamil et al. (2000) also reported, on the basis of collections in 1999, that *Trichogloeopsis pedicellata* grew abundantly at two sites, Cayo Lobo, Fajardo, at 5.0 m and Cayo Luis Peña, Culebra Island, at 3.0–7.0 m depths in eastern Puerto Rico.

Liagoropsidaceae S.M.Lin, Rodr.-Prieto et Huisman

Liagoropsis Yamada

Liagoropsis Yamada 1944:19.

Lightly calcified and lubricous axes are compressed or cylindrical. Thalli reach to 35 cm or greater in height. Branching is pinnate, dichotomous or paniculate. Structurally, thalli possess longitudinal medullary filaments that give rise to ditrichotomously dividing assimilatory filaments. Assimilatory filaments are cylindrical proximally, becoming moniliform distally. Spermatangia are borne in clusters, apically by assimilatory filaments. Carpogonial branches, straight and 4–8 cells long, are considered to be either accessory in nature or arising in normal branch positions. Gonimoblast initials are cut off directly from the fertilized carpogonium. Gonimoblast filaments are few and mostly lack sterile filaments; carpospores are produced from the developing filaments during maturation and subsequently are cut off terminally. Cystocarps are involucrate. One of the two recognized *Liagoropsis* species is known from Puerto Rico.

Liagoropsis schrammii (P.Crouan et H.Crouan) Doty et I.A.Abbott

FIGURE 50

Liagoropsis schrammii (P.Crouan et H.Crouan) Doty et I.A.Abbott 1964: 447, figs. 1–19.

Basionym: *Helminthocladia schrammii* P.Crouan et H.Crouan in Mazé and Schramm 1878: 177.

Homotypic Synonym: Nemalion shrammii (P.Crouan et H.Crouan) Børgesen 1909: 4, pl. I.

Puerto Rican Records: As *Nemalion shrammii*: Díaz-Piferrer 1963. As *Liagoropsis schrammii*: Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, Martinique, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: "Capesterre (Plage du port)"; Guadeloupe, West Indies, fide Mazé and Schramm 1878.

Highly lubricous thalli reach to 35 cm tall. Principal axes originate proximally, and branching is irregularly radial; branches are frequently proliferous. The branches are strongly contracted at their origin, becoming terete, compressed, or convolute and 1.5 cm diam. The branches taper distally. The medulla is composed of loose interwoven, thick-walled filaments, 2.0–12 µm diam. The assimilatory filaments composed of oval or moniliform cells, ~14 µm diam. and 28 µm long. Carpogonial branches are (3–)4(–6) cells long. Carposporangia measure ~11 µm diam. Algae are reddish brown in color.

Habitat and Comments: In the La Parguera area, the species has most frequently been collected at 2.0 to 3.0 m depth in *Thalassia* beds off Pitahaya. Doty and Abbott (1964)

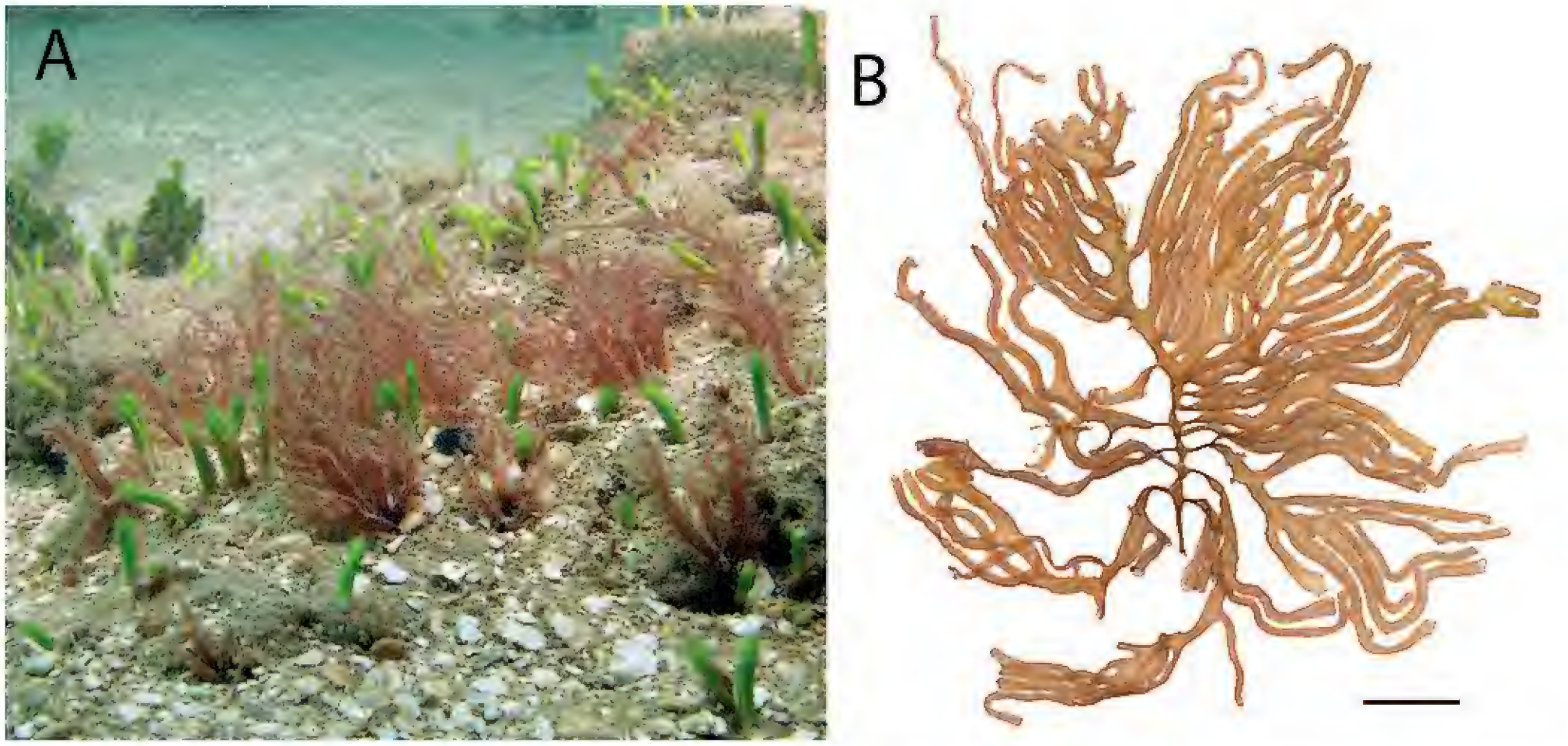

FIGURE 50. *Liagoropsis schrammii*. (A) In situ habit photograph, seagrass bed in front of Pitahaya. Field is approximately 20 cm. (B) DLBsn, herbarium specimen, seagrass bed in front of Pita Haya. Scale bar = 2.0 cm.

regarded the species to be synonymous with *L. maxima* Yamada; however, Lin et al. (2015) felt that further study was required. [Additional illustrations: Doty and Abbott 1964: figs. 1–19.]

Scinaiaceae Huisman, J.T.Harper et G.W.Saunders

Scinaia Biv.

Scinaia Biv. 1822: 232 [Bivona-Bernardi 1822].

Thalli are lubricous but have a firm texture. Thalli are composed of repeatedly dichotomously branched segments that are terete, complanate, or flat. The medulla is composed of longitudinal axial filaments embedded in mucilage. The cortex consists of an inner filamentous layer, an intermediate layer of a variable number of subcortical cells, and an outer layer of large terminal cells that are polyhedral in surface view. The polyhedral cells are laterally coherent and form a continuous epidermis. Reproductively, *Scinaia* demonstrates an alternation of heteromorphic generations, and gametophytes are monoecious or dioecious. Spermatangia occur in small surface sori. Carpogonial branches are 3-celled, and cystocarps occur within the inner cortex. Gonimoblasts give rise to terminal chains of carposporangia. Tetrasporophytes are filamentous. A single species of the 45 recognized species of *Scinaia* is known from Puerto Rico.

Scinaia complanata (Collins) Cotton

FIGURE 51

Scinaia complanata (Collins) Cotton 1907: 260.

Basionym: *Scinaia furcellata* f. *complanata* Collins in Collins et al. 1901: P.B.-A. no. 836.

Puerto Rican Records: As *Scinaia complanata*: Díaz-Piferrer 1963; Almodóvar 1965; Almodóvar and Ballantine 1983; Ballantine 1984; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Costa Rica, Caribbean Mexico, United States (North Carolina, Florida), Bermuda, Costa Rica, Cuba, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Indian River Inlet, Florida, USA.

Soft and somewhat lubricous thalli reach 5.0–8.0 cm tall. Terete to compressed axes are 7–9 times dichotomous. Axes measure 1.5–6.0 mm diam., and branching axils are broad and not normally constricted; branch apices are obtuse. An obscure medulla consists of a strand of 6–8(–30) slender filaments, to 4.0 µm diam. The cortex is made up of an inner pigmented layer of round or pyriform cells and a nonpigmented epidermis of cells, 12–44 µm diam. When viewed in section, cells of the epidermis are rectangular, 22 µm wide and 34–35 µm tall. Gametophytic algae are monoecious. Spermatangia occur in patches situated

FIGURE 51. *Scinaia complanata*. In situ habit photograph, seaward Media Luna Reef, 17 m. Field is approximately 15 cm.

between epidermal cells. Situated within the cortex, cystocarps measure 145–350 µm diam. and are enclosed by a 2–3-layered pericarp. Ovoid carposporangia are cut off in short chains and measure 4.0–5.0 µm diam. and 7.0–12 µm long. Algae are pale rose red in color.

Habitat and Comments: *Scinaia complanata* is found at moderate depths to deep water and is very common in the offshore Puerto Rican algal plains. [Additional illustrations: Setchell 1914: pl. 11: figs. 19–22; Feldmann 1939: fig. 9; Joly et al. 1963: pl. 1; Cormaci et al. 2017: FP174, figs. 3–5.]

Rhodymeniophycidae G.W.Saunders et Hommers.

Acrosymphytales Withall et G.W.Saunders

Acrosymphytaceae S.C.Lindstrom

Acrosymphyton G.Sjöstedt

Acrosymphyton G.Sjöstedt 1926: 8.

Thalli are uniaxial and lubricous. Branches are radially alternate, and axes are terete or slightly compressed. The medulla consists of central axial files of cells that are loosely surrounded by rhizoidal filaments. Medullary axial cells give rise to 4 assimilatory filaments that comprise the cortex. Terminal cells of the assimilatory filaments are moniliform. In cases where a sporangial generation is known, life histories involve an alternation of heteromorphic generations. Gametophytes are either monoecious or dioecious. Spermatangia are formed on terminal and subterminal cells of the assimilatory filaments. Carpogonial branches, 7–12 cells in length, are bilaterally branched and originate in the lower dichotomies of the assimilatory filaments. Auxiliary cells are terminal on typically unbranched moniliform filaments. Cystocarps are small and compact, with all gonimoblast cells developing into carposporangia. Tetrasporophytes are crustose *Hymenoclonium*-like forms and develop cruciate tetrasporangia. Six *Acrosymphyton* species are recognized worldwide; one of these is known from Puerto Rico.

Acrosymphyton caribaeum (J.Agardh) G.Sjöstedt

FIGURE 52

Acrosymphyton caribaeum (J.Agardh) G.Sjöstedt 1926: 9.

Basionym: *Calosiphonia caribaeum* J.Agardh 1899: 84.

Puerto Rican Records: As *Acrosymphyton caribaeum*: Ballantine and Norris 1989; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: United States (Florida), Bermuda, Puerto Rico, Saba Bank, Brazil.

Type Locality: Bermuda.

Bushy thalli, reaching to 20 cm in height, are highly lubricous. Primary axes develop proximally, and branching is 5–6 times radially alternate. Branches are 5.0–8.0 mm diam., decreasing to less than 1.0 mm diam. Axial filaments measure 60–130 µm diam., and whorled cortical assimilatory filaments in the larger branches are cut off near the middle of the axial cell. The assimilatory filaments are 5–7 times branched with distal cells, moniliform or obovate, 6.5–10 µm diam. Axial cells and proximal assimilatory cells give rise to rhizoids, to 7.0 µm diam., that grow into the medulla. Puerto Rican gametophytes are monoecious. Spermatangia, 2.0–3.0 µm diam., occur on outer cortical cells. The strongly curved carpogonial branches are 7–9 cells long and bear 1–4-celled lateral branchlets, from most of the carpogonial branch cells. Carpogonia possess elongate and spiraling trichogynes. Auxiliary cell branches, 5–12 cells long, occur independently of the carpogonial branches and bear a single terminal auxiliary cell, 12–14 µm diam. The cystocarps measure 45–90 µm diam. Algae are light red in color.

Habitat and Comments: *Acrosymphyton caribaeum* grows solitarily, or occasionally, a few individuals occur in proximity. In Puerto Rico, the species has been collected at depths of 9.0–17 m. In the field *Acrosymphyton* and the more common *Dudresnaya* are difficult to distinguish; however, microscopic examination reveals reproductive differences. [Additional illustrations: Ballantine and Norris 1989: figs. 3, 5; Guimarães and Amado-Filho 2008: figs. 1–9.]

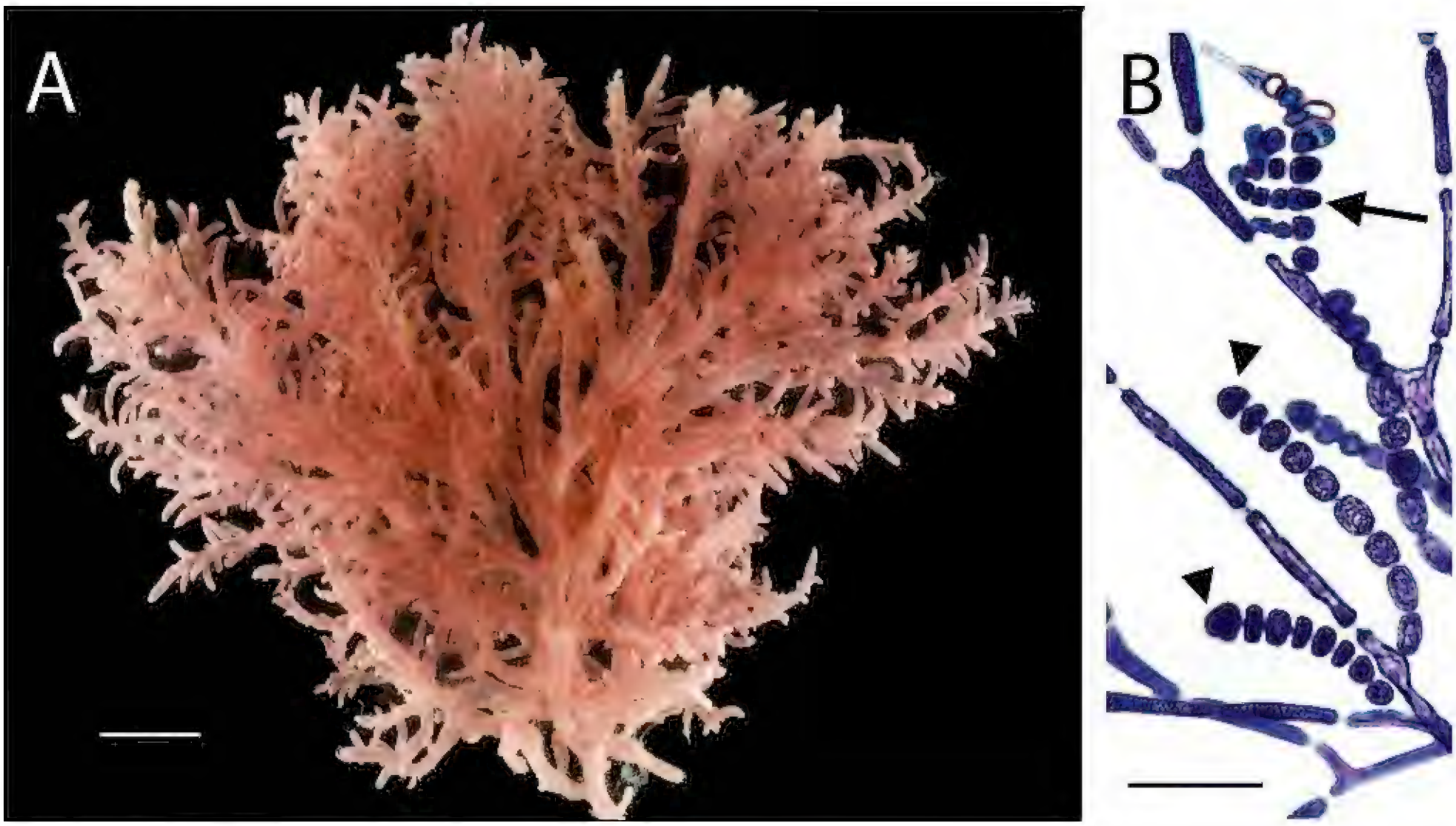

FIGURE 52. *Acrosymphyton caribaeum*. (A) Live specimen, algal plain seaward Media Luna Reef, 17 m. Scale bar = approximately 2.0 cm. (B) Photomicrograph of cortical filaments bearing a carpogonial branch (arrow) with lateral branches from carpogonial branch cells and auxiliary cell branches with terminal auxiliary cells (arrowheads). Scale bar = 50 µm.

Bonnemaisoniales Feldmann et Feldm.-Maz.

Bonnemaisoniaceae F.Schmitz

Asparagopsis Mont.

Asparagopsis Mont. 1840: xv [Montagne 1840].

Gametophytic thalli have stoloniferous bases that give rise to erect percurrent axes with numerous determinate laterals that have a soft and feathery or plumose appearance. Gametophytes are dioecious. Spermatangia are formed in sori on short branchlets that are cut off by the indeterminate axes. Carpogonial branches are 2–4-celled, also formed in branchlets borne on indeterminate axes. Ovoid to subglobose cystocarps are pedicellate. The life history involves an alternation of heteromorphic generations. The sporangial or *Falkenbergia* stage is uniaxial filaments with 3 periaxial cells. The filaments are alternately to irregularly branched and partially erect. Tetrasporangia are cruciately divided. One of the three recognized *Asparagopsis* species is reported from Puerto Rico.

Asparagopsis taxiformis (Delile) Trevis.

FIGURE 53

Asparagopsis taxiformis (Delile) Trevis. 1845: 45.

Basionym: *Fucus taxiformis* Delile 1813: 295, pl. 57: fig. 2.

Heterotypic Synonym: Falkenbergia hillebrandii (Bornet) Falkenb. 1901: 689–690.

Puerto Rican Records: As *Asparagopsis taxiformis*: Díaz-Piferrer 1963; Almodóvar 1964a, 1965; Almodóvar and Ballantine 1983; Ballantine et al. 1987, 2001, 2011, 2016b; Ballantine and Aponte 1997a; Ní Chualáin et al. 2004. As *Falkenbergia hillebrandii*: Almodóvar and Blomquist 1959; Almodóvar and Biebl 1962; Navarro and Almodóvar 1974; Hinds and Ballantine 1987; Ballantine et al. 2001.

Western Atlantic Distribution: Belize, Costa Rica, Panama, Caribbean Mexico, United States (Georgia, Florida), Bermuda, Bahamas, Barbados, Bermuda, Costa Rica, Cuba, El Salvador, Hispaniola, Jamaica, Martinique, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Alexandria, Egypt.

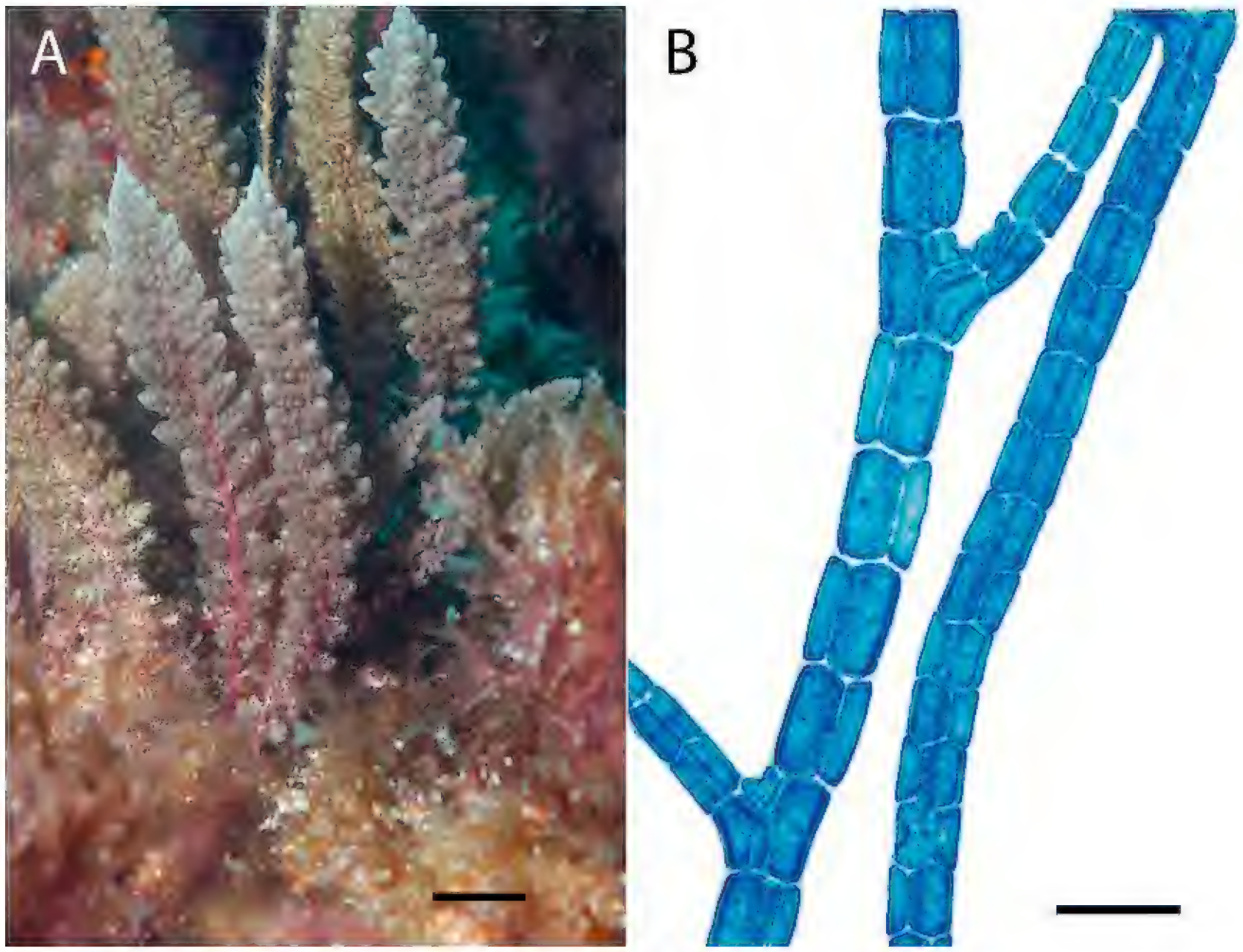

FIGURE 53. *Asparagopsis taxiformis*. (A) In situ habit photograph, seaward Media Luna Reef, La Parguera, 17 m. Field is approximately 10 cm. (B) Photomicrograph of *Asparagopsis* life history alternate, *Falkenbergia hillebrandii*. Scale bar = 100 µm.

Gametophytic thalli are pyramidal, soft in texture, and plumose. Axes reach 5.0–20 cm or more in height from an entangled rhizomatous base. Erect axes are clothed by numerous determinate slender branchlets, ~250 µm in diameter and 2.0–5.0 cm long, and may be with or without a few lateral branches proximally. Lateral branchlets, when present, divide frequently and taper distally; the last order branchlets of 3 rows of cells. Anatomically, the principal axes possess axial filaments that give rise to opposite filaments. A medullary cavity is surrounded by a cortex formed by filaments cut off by proximal cells of the lateral branchlets. Sporophytes in Puerto Rico are represented by a "*Falkenbergia* stage." The mostly prostrate-growing sporophytes reach 2.0 cm tall and comprise alternately branched filaments, 30–80 µm diam., with cells 0.5–1.2 diameters long. The filaments appear to possess 3 pericentral cells. Spherical cystocarps measure 400–550 µm diam. and are pedicellate, situated terminally on branchlets. Tetrasporangia occur solitarily on branchlets. Gametophytes are purple violet or grayish in color, and sporophytes are pinkish to brick red.

Habitat and Comments: Both gametophytic and sporophytic phases of *Asparagopsis taxiformis* are common in Puerto Rico. The species has been observed in abundance at the offshore algal plains and at Bahia Sucia on Puerto Rico's southern coast. The "*Falkenbergia*" phase is very commonly seen as pink tufts in shallow-water environments, particularly on mangrove prop roots. On the basis of molecular sequences, Ní Chualáin et al. (2004) suggested that Caribbean *A. taxiformis* may represent a new species or subspecies. On the basis of their mitochondrial molecular sampling, Andreakis et al. (2007) subsequently concluded that *A. taxiformis* currently comprises three biological but cryptic (morphologically similar) species. *Asparagopsis taxiformis* is considered to be a highly invasive species, with introduction reported to be from the Mediterranean (Zanolla et al. 2014). *Asparagopsis* is well known to synthesize brominated compounds (McConnell and Fenical 1977). [Additional illustrations: Littler and Littler 2000: 66; Ní Chualáin et al. 2004: fig. 6; Braune and Guiry 2011: fig. 121.2.]

Naccariaceae Kylin

Naccaria Endl.

Naccaria Endl. 1836: 6.

Thalli are bushy and gelatinous, originating from a discoid holdfast. Erect axes are terete, and branching is irregular. Obliquely divided apical cells give rise to a monosiphonous axes. The central axis cuts off spirally positioned, short, lateral, deciduous, pigmented filaments. Proximal lateral filament cells give rise to downwardly directed rhizoids that develop into a pseudoparenchymatous cortex. In older thalli, the parenchymatous cortex may separate partially from the central axial filament. Gametophytes are dioecious. Spermatangia are borne in clusters at the base of the assimilatory filaments. Carpogonial branches are 2(–4)-celled, and cystocarps are located medially or distally on assimilatory filaments. Carposporangia are formed terminally on gonimolobes. One of the five recognized *Naccaria* species occurs in Puerto Rico.

Naccaria corymbosa J.Agardh

FIGURE 54

Naccaria corymbosa J.Agardh 1899: 109.

Puerto Rican Records: Ballantine et al. 2019.

Western Atlantic Distribution: United States (North Carolina, Florida), Bermuda, Puerto Rico, Brazil.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Key West, Florida Keys, Florida, USA.

Thalli are bushy, to 15 cm tall and lubricous in texture. The principal axes measure to 1.0 mm diam.; uncorticated axes measure 30–100 µm. Branching is radially alternate, and axes are terete. Axial cells measure 4.0–6.0 µm diam. and 90–200 µm long. Lateral branches are frequently deciduous. Central axial cells cut off 2 periaxial cells, 80–100 µm diam., per segment that give rise to cortical filaments, 27–40(–150) µm long. Lower (jacket) cells of the cortical filaments are elongate oval-shaped, becoming oval to terete. Plastids are distinctively ribbonlike and highly conspicuous in the jacket cells. The jacket cells cut off numerous descending slender rhizoids, resulting in heavy cortication. Gametophytes are dioecious. Carpogonial branches, 3- to 4-celled, are tightly reflexed, with the periaxial cell being the support cell. Two-celled sterile groups are borne on carpogonial branch cells. Ovoid carposporangia, 10–13 µm diam. and 17–20 µm long, are terminally borne by gonimolobes.

Habitat and Comments: The first record of *Naccaria corymbosa* for the Caribbean was a single specimen from 17 m depth at the algal plain offshore from Media Luna Reef

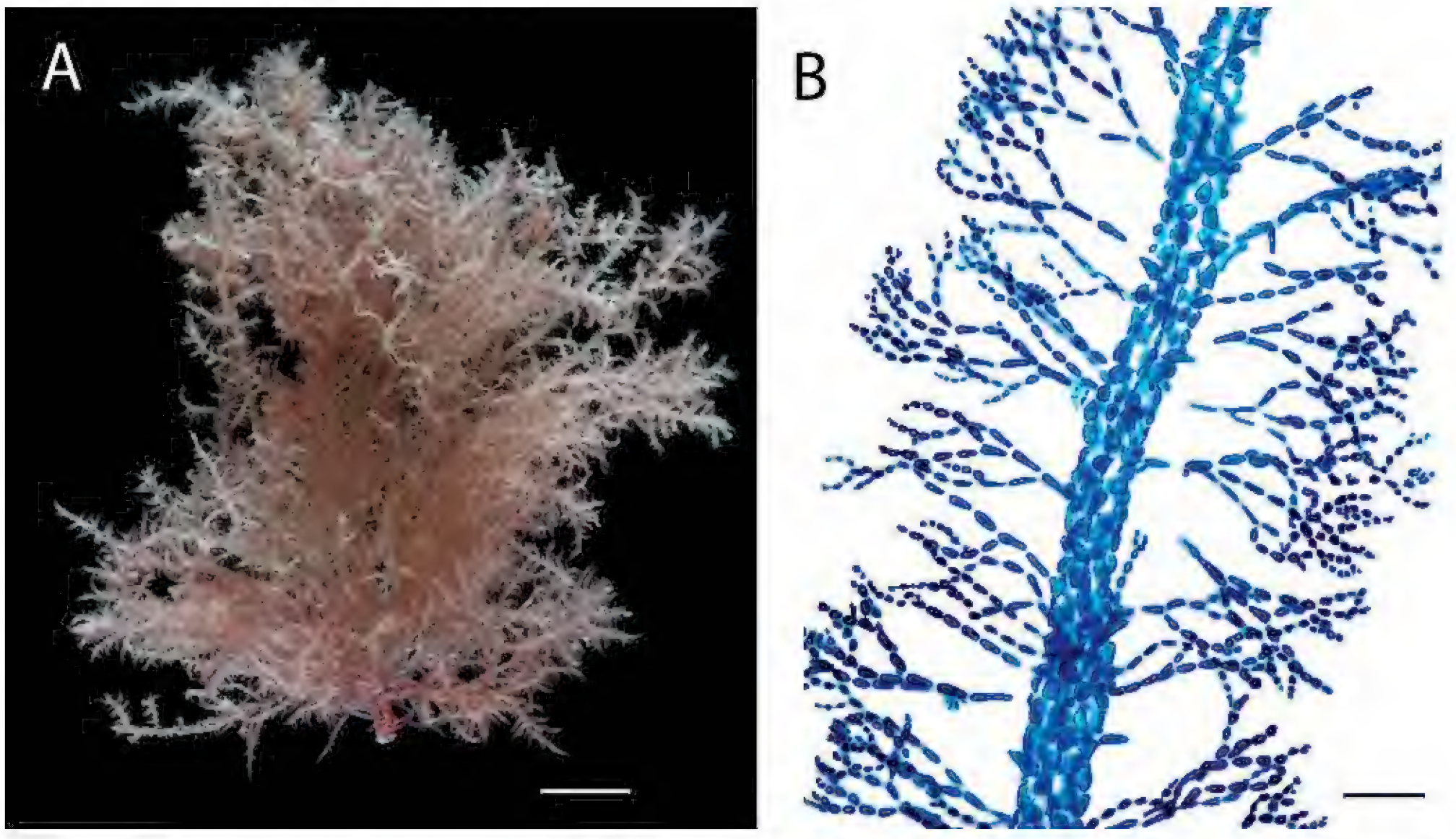

FIGURE 54. *Naccaria corymbosa*. (A) DLB7290, habit of live specimen, 1.5 km seaward Media Luna Reef, 17 m. Scale bar = 1.0 cm. (B) DLB7290, corticated axis with lateral assimilatory filaments. Scale bar = 100 µm.

(Ballantine et al. 2019). *Naccaria corymbosa* bears close resemblance to the genus *Reticulocaulis*, differing by the number of carpogonial branch cells (9–13 in *Reticulocaulis* and 2–8 in *Naccaria*) and degree of development of sterile laterals (less developed in *Naccaria*). [Additional illustrations: Guimarães and Amado-Filho 2008: figs. 18–26.]

Atractophorales Le Gall, Filloramo et G.W.Saunders

Atractophoraceae Maggs, Le Gall et G.W.Saunders

Liagorothamnion Huisman, D.L.Ballant. et M.J.Wynne

Liagorothamnion Huisman, D.L.Ballant. et M.J.Wynne 2001: 507–508.

Thalli are filamentous and erect. Axial cells give rise to 1 indeterminate lateral branch and 1 to 4 whorl branchlets per axial cell. Plastids are ribbonlike. Spermatangial branches are much divided, in whorls on successive axial cells. Carpogonial branches are 3–4-celled and strongly curved, borne on an intercalary axial cell. The support cell has 2 to 3 sterile groups. Basal cells of whorl branchlets on the fertile axial cell (excluding the supporting cell) function as auxiliary cells. Carposporophytes are globular, with almost all gonimoblast cells becoming quadripartite carposporangia. *Liagorothamnion* is a monotypic genus.

Liagorothamnion mucoides Huisman, D.L.Ballant. et M.J.Wynne

FIGURE 55

Liagorothamnion mucoides Huisman, D.L.Ballant. et M.J.Wynne 2001: 508–509, figs. 1–19.

Puerto Rican Records: Huisman et al. 2001.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Leeward Media Luna Reef, La Parguera, Puerto Rico.

Highly lubricous thalli reach 8.0 cm in height, with axes to 1.0 mm diam. Axial cells measure 5.0–10 µm diam. near the apices, increasing to >200 µm diam. Each axial cell gives rise to 1 indeterminate lateral and 1–4 determinate whorl branchlets. The whorl branchlets are generally simple, 4.0–7.0 µm diam. and 1–15 cells long. Primary axes are secondarily corticated by rhizoids that issue from lower cortical cells. Spermatangia branches occur in whorls on 3–16 successive axial cells. Carpogonial branches are 3–4–celled. Cystocarps are globular and measure 150–360 µm diam. Carposporangia are subspherical, 10–12 µm diam., with quadripartite division. Tetrasporophytic thalli are unknown.

Habitat and Comments: Algae bear a very strong resemblance to *Liagora* in the field. Despite the appearance of calcification, the specimens are probably not calcified, the calcified appearance being due to the adherence of detritus to the mucilage. The species was described from an inshore habitat in La Parguera, Puerto Rico (Huisman et al. 2001), and has not been collected outside of its type locality. Initially, the genus was incorrectly placed in the Ceramiaceae (largely due to its superficial resemblance to *Dohrniella*), and it was subsequently placed in the Naccariaceae by Schneider and Wynne (2007). Saunders et al. (2016) subsequently placed the genus in the Atractophoraceae.

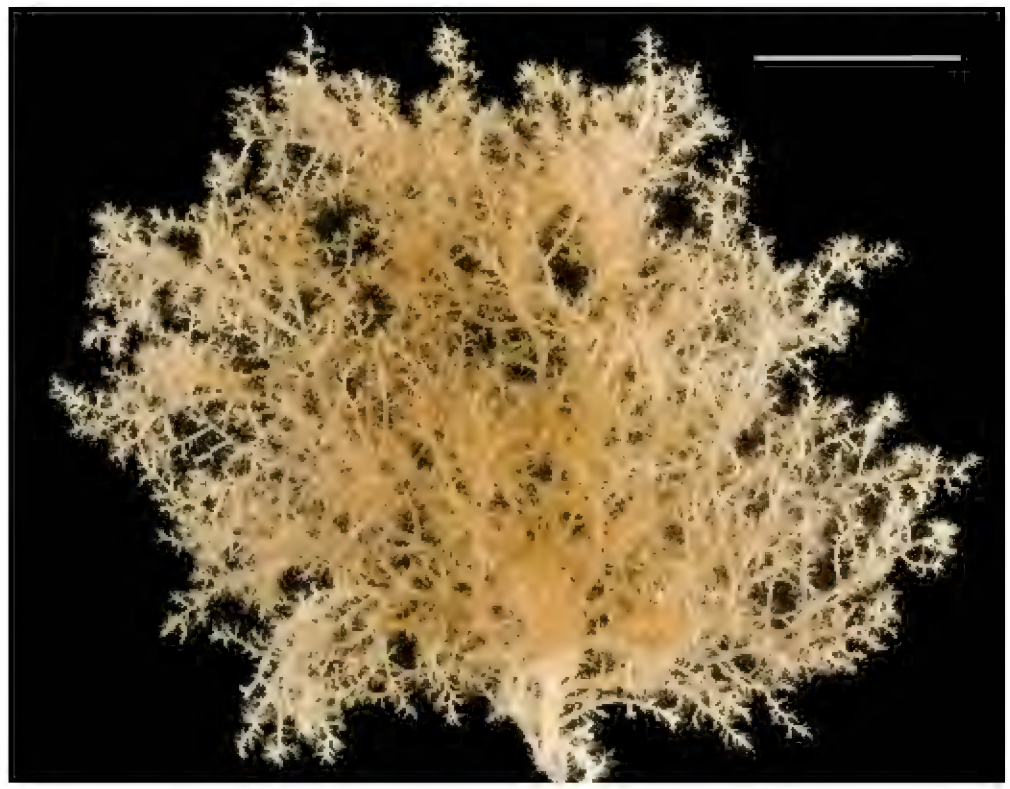

FIGURE 55. *Liagorothamnion mucoides*. DLB7204, herbarium specimen, leeward Media Luna Reef, 1.0 m. Scale bar = 2.0 cm.

Gelidiales Kylin

Gelidiaceae Kütz.

Gelidium J.V.Lamour.

Gelidium J.V.Lamour. 1813: 126, nom. et typ. cons.

Cartilaginous thalli are 2.0 to 40 cm in height. Erect terete or compressed axes are distichously or irregularly branched and are produced by creeping axes. Prostrate axes are attached by disklike holdfasts. Axes are uniaxial, developing from a single apical cell. Appearing round in section, colorless medullary cells, to 30 µm diam., are either loosely or tightly appressed. Outward from the medulla is a cortex of several layers of pigmented cells, 2.0–15 µm diam. Thick-walled rhizines, to 200 µm long, run transversely in the medulla and cortex. Rhizine position varies among species. Spermatangia, cut off from outer cortical cells, develop as patches on branches of male gametophytes. Carpogonial branches are 3 cells long, and gonimoblasts develop directly from the fertilized carpogonium. Bilocular carposporophytes are up to 1.0 mm long. Ovoid cruciate tetrasporangia,

30–45 µm diam., occur in sori in frequently expanded tips of lateral branches.

Note: *Gelidium* has long been considered to be taxonomically difficult, due in part to substantial morphological plasticity. This is true to such an extent that Dixon and Irvine (1977: 138) quoted Bornet's reference to *Gelidium* as the "genre diabolique." There are five *Gelidium* species in Puerto Rico; 145 species are recognized worldwide.

KEY TO THE *GELIDIUM* SPECIES OF PUERTO RICO

1. Rhizines limited to the medulla 2
   Rhizines present in medulla and inner cortex 3
2. Thalli to 6 cm tall; erect axes flattened, to 1.0 mm broad . . . . . *G. americanum*
   Thalli 2–5(–15) cm tall; erect axes terete to compressed, 0.5–0.75 mm broad . . . . . *G. pusillum*
3. Erect axes subterete, ~0.5 mm wide . . . . . *G. crinale*
   Erect axes compressed to flat 4
4. Erect axes 1.0 mm wide . . . . . *G. floridanum*
   Erect axes 0.5–2.0 mm wide . . . . . *G. corneum*

Gelidium americanum (W.R.Taylor) Santel.

FIGURE 56

Gelidium americanum (W.R.Taylor) Santel. 1976: 173, figs. 28–33.

Basionym: Pterocladia americana W.R.Taylor 1943: 154, pl. 4: fig. 1.

Puerto Rican Records: As *Gelidium americanum*: Ballantine and Aponte 1997a, 2002a. As *Pterocladia americana*: Díaz-Piferrer 1963; Díaz-Piferrer and Caballer de Pérez 1964; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Perrone et al. 2019.

Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina, South Carolina, Florida), Bermuda, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Port Antonio, Jamaica.

FIGURE 56. *Gelidium americanum*. DLB6982, herbarium specimen, Ballena Bay, Guánica, 1.0–2.0 m. Scale bar = 1.0 cm.

Thalli arise from a subterete stoloniferous base. Flattened erect primary axes, to 6.0 cm in height and 2.0 mm wide, are simple, irregular, or sparingly pinnately branched to 4 orders. Rhizines occur sparsely, principally in the central medullary region. Constricted branchlets are subcylindrical proximally and become flattened, to 1.0 mm wide and 75–150 µm thick, distally. Thick-walled rhizines, 3.0–6.0 µm diam., are interspersed among slender medullary cells, 10–20 µm diam. Carposporophytes occur in swollen branchlets. Tetrasporangia, 30–45 µm diam., occur in sori in branchlets of the ultimate branching orders. Algae are dark maroon in color.

Habitat and Comments: Littler and Littler (2000) indicated that *Gelidium americanum* typically occurs in wave-impacted intertidal environments as well as to 8.0 m deep. Thalli tend to be taller and branched to a further degree when living in sheltered habitats. [Additional illustrations: Littler and Littler 2000: 43; Perrone et al. 2019: figs. 28–32.]

Gelidium corneum (Huds.) J.V.Lamour.

FIGURE 57

Gelidium corneum (H.J.Huds.) J.V.Lamour. 1813: 129.

Basionym: *Fucus corneus* H.J.Huds. 1762: 474.

Puerto Rican Records: As *Gelidium corneum*: Almodóvar 1964a, 1964b, 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: United States (Florida, South Carolina, Texas), Bermuda, Cuba, Martinique, Mexico, Panama, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Uruguay, Venezuela.

World Distribution: See Guiry and Guiry 2024

Type Locality: Devonshire, England.

FIGURE 57. *Gelidium corneum*. LRA4995, herbarium specimen, Yabucoa, intertidal. Scale bar = 1.0 cm.

Gelidium corneum is the generitype. Thalli are bushy and cartilaginous, reaching 2.0–50 cm in height. Prostrate axes are attached by rhizoids. Erect axes are flattened, 0.5—2.0 mm broad, and pinnately branched. Branchlets are slightly constricted proximally, and apices are obtuse. Female gametophytes tend to be twice pinnate, and the sporophytic thalli are less branched. Rhizines are mostly located in the outer medulla and inner cortex.

Habitat and Comments: Puerto Rican specimens attributed to *Gelidium corneum* have been collected in shallow-water, protected habitats. Silva et al. (1996) considered the name *Gelidium corneum* to be ambiguous and felt it should be applied to European *Gelidium sesquipedale* (Clemente) Thuret. Taylor (1960) also expressed skepticism over many of the western Atlantic identifications of this species. [Additional illustrations: Børgesen 1916: fig. 124; Kim and Hwang 2015: figs. 11–14.]

Gelidium crinale (Hare ex Turner) Gaillon

FIGURE 58

Gelidium crinale (Hare ex Turner) Gaillon 1828: 362.

Basionym: Fucus crinalis Hare ex Turner 1819: 4, figs. c,e–g.

Puerto Rican Records: As *Gelidium crinale*: Almodóvar and Blomquist 1965; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a; Kim and Boo 2012; Perrone et al. 2019.

Western Atlantic Distribution: Caribbean Mexico, United States (Maine, Massachusetts, Virginia, North Carolina, Florida), Bermuda, Barbados, Cuba, Hispaniola, Jamaica, Puerto Rico, Trinidad and Tobago, Argentina, Brazil, Colombia, Uruguay.

World Distribution: See Guiry and Guiry 2024.

Lectotype Locality: Ilfracombe, Devonshire, England, fide Dixon and Irvine 1977: 140.

Algae occur in dense tufts, 2.0–5.0 cm in height. Thalli possess prostrate axes, ~0.5 mm diam., that spread over the substratum and are attached by rhizoidal holdfasts. The erect subterete axes, 1.5–7.0 cm in height, are irregularly alternately branched below and pinnately branched above. Branch apices are acute. Grouped rhizines are present throughout the medulla. The cortex is composed of cells, 15–16 µm diam. Gametophytes are dioecious. Spermatangia occur on the surface of branchlets. Globose to bilocular carposporophytes, 360–550 µm diam., occur in locally enlarged branchlets. Clavate carpospores measure 11–30 µm diam. and 32–80 µm long. Sporophytic thalli have flattened to spathulate branches, and tetrasporangia

FIGURE 58. *Gelidium crinale*. DLB7586, herbarium specimen, Ballena Bay, Guánica, 1.0 m. Scale bar = 1.0 cm.

measure 10–78 µm diam. Algae are dull purplish to yellowish brown in color.

Habitat and Comments: In Puerto Rico, specimens ascribed to *Gelidium crinale* have been collected in the intertidal as well as shallow water at Ballena Bay. Perrone et al. (2019) cite numerous examples of confused *Gelidium crinale* identifications. Although *G. crinale* was treated as being synonymous with *G. pusillum* by Dixon and Irvine (1977), Womersley and Guiry (1994) concluded that the types of the two entities were distinct. Nevertheless, Kim and Boo (2012) further stated that separation of *G. crinale* from *G. pusillum* on morphological bases alone is problematic and that molecular analyses are required for confirmation. [Additional illustrations: Cordeiro-Marino 1978: figs. 61–63; Littler et al. 2008: 100; Croce and Parodi 2013: figs. 1–49; Kim and Boo 2012: fig. 5; Diaz-Tapia and Bárbara 2014: figs. 114–131; Kim and Hwang 2015: figs. 15, 16.]

Gelidium floridanum W.R.Taylor

Gelidium floridanum W.R.Taylor 1943: 153, pl. III: figs. 1, 2.

Puerto Rican Records: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: United States (Florida), Bermuda, Costa Rica, Cuba, Puerto Rico, Trinidad and Tobago, Brazil, Venezuela.

Type Locality: Indian River, Florida, USA.

Thalli possess branched, entangled filaments below. Strap-shaped erect axes, ~1.0 mm wide, are to 13 cm in height. The erect axes are pinnately and distichously branched. Branchlets are contracted at the base and are obtuse apically. Rhizines are abundant, occurring in scattered groups in the medulla and cortical regions. Fertile branchlets are located in the lower branchlets cut off from the primary axes. Female branchlets give rise to 1(–2) bilocular carposporophytes. Tetrasporangia occur centrally within fertile branchlets.

Habitat and Comments: The record of *G. floridanum* in Puerto Rico is based on a single intertidal collection, FPDB3165 (MSM), from Cabo Rojo (Díaz-Piferrer 1963). *Gelidium floridanum* is considered to be rare within its distribution. However, Thomas and Freshwater (2001) speculate that the species may be more widely distributed within the region, as it has been misidentified as "*G. capillacea*" (=*G. capillaceum* (S.G.Gmelin) Menegh., which is now *Pterocladiella capillacea* (S.G.Gmelin) Santel.et Hommers.). [Illustrations: Cordeiro-Marino 1978: figs. 70–77; Littler et al. 2008: 101; Thomas and Freshwater 2001: figs. 7–12.]

Gelidium pusillum sensu W.R.Taylor

Gelidium pusillum sensu Taylor 1960: 354–355, pl. 45: fig. 4 [non *Gelidium pusillum* (Stackh.) Le Jolis 1863: 13; *Fucus pusillus* Stackhouse 1795: 16, pl. 6].

Puerto Rican Records: As *Gelidium pusillum* sensu Taylor 1960; Díaz-Piferrer 1963; Almodóvar 1965; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Costa Rica, Caribbean Mexico, United States (North Carolina, Florida), Bermuda, Martinique, Puerto Rico, Trinidad and Tobago, Barbados, Brazil, Colombia, Venezuela, Argentina, Uruguay.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Sidmouth, Devon, England.

Thalli with repent, creeping axes below giving rise to erect strap-shaped blades reaching 5.0–15 mm in height. The erect axes are subcylindrical proximally and becoming flattened, 0.5–0.75 mm above. Little-branched blades are pinnate; branch tips are acute apically. The medulla is composed of cells to 25 µm diam. Rhizines, 4.0–10 µm diam., are located subcortically or are absent. Carposporangia are biloculate and occur distally on short branchlets. Cruciately divided tetrasporangia, 25–40 µm diam., are also distally positioned in branchlets.

Habitat and Comments: *Gelidium pusillum* typically occurs in the upper regions of the intertidal. Perrone et al. (2019) reported that the name "*G. pusillum*" has historically been misapplied to many small specimens of *Gelidium* worldwide and concluded that the species is limited in its distribution to the North Atlantic. See Kim and Boo (2012) under comments on *G. crinale* above. Puerto Rican specimens need to be morphologically and genetically studied to determine their taxonomic position. [Illustrations: as "*Gelidium pusillum*", Taylor 1960: fig. 4; Egerod 1971: figs. 32–49.]

Gelidiellaceae K.-C. Fan

Gelidiella Feldmann et Hamel

Gelidiella Feldmann et Hamel 1934: 529.

Thalli consist of prostrate and erect axes attached by clusters of rhizoids. Slender axes, cylindrical or compressed, are wiry in texture. Branching is variable; however, it is frequently distichous. Branches possess a prominent apical cell. Internally, algae possess a medulla of longitudinal filaments and a 1–3-celled cortical layer. Rhizines are absent. Reproductively, most species are known only as tetrasporophytes; however, a triphasic life history is assumed. Spermatangia occur in superficial sori, cut off from outer cortical cells. Tetrasporangia, tetrahedrally, cruciately, or irregularly divided, are situated in swollen branches. Fifteen *Gelidiella* species are recognized worldwide; one of these is known from Puerto Rico.

Gelidiella acerosa (Forssk.) Feldmann et Hamel

FIGURE 59

Gelidiella acerosa (Forssk.) Feldmann et Hamel 1934: 533.

Basionym: *Fucus acerosus* Forssk. 1775: 190.

Puerto Rican Records: Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1964a, 1964b; Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar 1965; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a; Thomas and Freshwater 2001; Ballantine and Aponte 2002a.

Western Atlantic Distribution: Belize, Costa Rica, Caribbean Mexico, Panama, United States (Florida), Bahamas, Bermuda, Cayman Islands, Cuba, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: "Mochhae" (Al Mukha, Yemen, fide Silva et al. 1996).

Thalli are cartilaginous, with decumbent and erect terete axes to 2.0 mm diam. and to 15 cm tall, sometimes recurved, and prostrate axes are attached by rhizoidal clusters. Branching is variable and may be alternate, simple, or bilateral. The unbranched lateral branches measure 2.0.0–6.0 mm long. The medulla is composed of dense, thick-walled longitudinal filaments and lacks rhizines. The medullary cells measure 10–25 µm diam. Carposporangia are located in somewhat swollen branchlets. Ellipsoidal tetrasporangia,

FIGURE 59. *Gelidiella acerosa*. DLB6508, herbarium specimen, Guajataca, intertidal. Scale bar = 1.0 cm.

8.0–9.0 µm diam. and ~15 µm long, occur in distally swollen branchlets. Algae are yellow to dark red in color.

Habitat and Comments: *Gelidiella acerosa* is quite common in intertidal and shallow habitats in Puerto Rico and has less commonly been collected to 17 m depth. [Additional illustrations: Santelices 2004: figs. 1, 6, 7, 12, 13, 18, 23; Lin and Freshwater 2008: figs. 13–19; Braune and Guiry 2011: fig. 116.1.]

Millerella G.H.Boo et S.M.Boo

Millerella G.H.Boo et S.M.Boo in Boo et al. 2016: 975.

Thalli possess prostrate and erect axes. The prostrate axes are terete and attached by clusters of unicellular rhizoids. Erect axes are terete to compressed or flattened. Apices possess a single apical cell. Tetrasporangia develop in apical regions of the erect and lateral branches. Subspherical tetrasporangia are cut off by periaxial cells. Six species of *Millerella* are recognized, of which one is known from Puerto Rico.

Comments: Although Boo et al. (2016) noted that gametophytes are unknown, earlier, Rico et al. (2002, as *Gelidiella tenuissima* Feldmann et Hamel) detailed male gametophyte morphology found in *Millerella pannosa*.

Millerella pannosa (Feldmann) G.H.Boo et LeGall

Millerella pannosa (Feldmann) G.H.Boo et LeGall in G.H.Boo et al. 2016: 975.

Basionym: Echinocaulon pannosum Feldmann 1931: 12.

Homotypic Synonym: Gelidiella pannosa (Feldmann) Feldmann et Hamel 1934: 534, figs. 1, 2, nom. inval.

Heterotypic Synonyms: Gelidium tenuissima Feldmann et Hamel 1936: 102, nom. inval.; as *Gelidiella tenuissimum:* Feldmann et Hamel, 1936: 102, figs. 11, 12, nom. illeg.; *Parviphycus tenuissimus* (Feldmann et Hamel) Santelices 2004: 324, figs. 21, 26, nom illeg.

Puerto Rican Records: As *Gelidium tenuissima*: Blomquist and Almodóvar 1961; Almodóvar and Ballantine 1983. As *Gelidiella pannosa*: Ballantine and Aponte 1997a. As *Parviphycus tenuissimus*: Santelices 2004.

Western Atlantic Distribution: Puerto Rico.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Biarritz, Pyrénées-Atlantiques, France.

Thalli form mats, 1.0–2.0 cm high, composed of both entangled stoloniferous and erect axes that are attached by unicellular rhizoids. Compressed to flattened erect, sparingly branched axes measure 1.0–2.0 mm long. Structurally, thalli have a central axis surrounded by 1–2 layers of thick-walled cells and an outer 1-celled thick cortex. Spermatangia occur in patch-like sori that cover both sides of the erect axes. Tetrahedrally divided tetrasporangia occur in enlarged flattened distal branches and are up to ~42 µm diam.

Habitat and Comments: *Millerella pannosa* was originally collected in Puerto Rico at Magueyes Island by L. R. Almodóvar as *Gelidium tenuissima*, growing as a dense felt on *Rhizophora mangle* prop roots. Gametophytic thalli are not known from Puerto Rico. [Illustrations: as *Gelidium tenuissimum*, Blomquist and Almodóvar 1961: figs. 1–10; as *Gelidiella tenuissima*, Joly et al. 1963: pl. 2: figs. 1–4; Rico et al. 2002: figs. 1–11.]

Pterocladiaceae G.P.Felicini et C.Perrone

Pterocladiella Santel. et Hommers.

Pterocladiella Santel. et Hommers. 1997: 117.

Thalli possess a base of tangled stolons that give rise to erect axes. The distally flattened erect axes are irregularly, alternately, or pinnately branched. Axes, with a single apical cell, are structurally composed of a medulla with thick-walled cells and a cortex of ~3 cell layers. The outermost cortical cells are slightly elongate anticlinally. Rhizines are found in the medulla and/or the cortex. Spermatangia occur in superficial sori on fertile branches. Carpogonia are intercalary on carpogonial branches, and following fertilization, gonimoblast filaments form a network with files of nutritive cells. Tetrasporangia are located in sori. There are two *Pterocladiella* species in Puerto Rico; 24 species are recognized worldwide.

KEY TO THE *PTEROCLADIELLA* SPECIES OF PUERTO RICO

1. Thalli 6–8 cm tall; branching usually once pinnate; axes 0.5 mm broad. . . . . ***P. bartlettii***
   Thalli 5–20 cm tall; branching 3–4 times pinnate; axes 1–2 mm broad . . . . . ***P. capillacea***

Pterocladiella bartlettii (W.R.Taylor) Santel.

FIGURE 60

Pterocladiella bartlettii (W.R.Taylor) Santel. 1998: 242.

Basionym: *Pterocladia bartlettii* W.R.Taylor 1943: 156.

Puerto Rican Records: As *Pterocladiella bartlettii*: Ballantine and Aponte 2002a. As *Pterocladia bartlettii*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a; Santelices 1998.

Western Atlantic Distribution: Costa Rica, Caribbean Mexico, North America, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

FIGURE 60. *Pterocladiella bartlettii*. DLB5226, herbarium specimen, Cabo Rojo lighthouse, 0.5–1.0 m. Scale bar = 1.0 cm.

FIGURE 61. *Pterocladiella capillacea*. LRA5118, Guardarraya, on rocks in shallow water. Scale bar = 1.0 cm.

Type Locality: Saint Louis du Sud, Haiti.

Thalli reach up to 8.0 cm in height, arising from entangled stolons, 100–230 µm diam. Erect axes are compressed and linear to spathulate, 80–300 µm diam., or flattened, 80–150 µm thick and 200–650 µm wide. Axes are alternately bilaterally branched to 4 branching orders. Flattened branches are terminally acute. The medulla has 1–5 layers of circular cells, 7.0–14 µm diam. Rhizines are abundant in the medullary region. Outside the medulla is a 1–3-celled cortex of circular, 7.0–13 µm diam., cells. Spermatangia are unknown. Cystocarps are unilocular, occurring singly, occasionally paired, distally in curved ultimate branchlets. Ovoid cruciately divided tetrasporangia are in stichidium-like enlargements of the branchlets, near the base of the thallus. Algae are dull purple in color.

Habitat and Comments: *Pterocladiella bartlettii* is somewhat uncommon in Puerto Rico, being known from shallow rocks at Cabo Rojo. [Additional illustrations: Taylor 1960: pl. 46: fig. 2; Thomas and Freshwater 2001: figs. 13–15; Iha et al. 2017: figs. 8–17.]

Pterocladiella capillacea (S.G.Gmel.) Santel. et Hommers.

FIGURE 61

Pterocladiella capillacea (S.G.Gmel.) Santel. et Hommers. 1997: 118, figs. 1a, 2b, 3b, 4, 5.

Basionym: *Fucus capillaceus* S.G. Gmelin 1768: 146, pl. 15: fig. 1 (lectotype illustration).

Heterotypic Synonym: *Pterocladia pinnata* (Huds.) Papenf. 1950: 192.

Puerto Rican Records: As *Pterocladiella capillacea*: Ballantine and Aponte 1997a, 2002a. As *Pterocladia pinnata*: Díaz-Piferrer 1963; Almodóvar 1964b; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Costa Rica, Caribbean Mexico, United States (Florida), Barbados, Hispaniola, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela, Uruguay, Argentina.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Locus, Mediterranean Sea.

Pterocladiella capillacea is the generitype. Erect and prostrate thalli are cartilaginous. Prostrate axes, 360–500 µm diam., possess peg-like fibrous holdfasts. Erect axes, cylindrical proximally and strap-like above, to 3.0 mm broad and to 150 µm thick, reach up to 5.0–20 cm in height. The erect principal axes possess an ill-defined costa proximally and are 3–4 times pinnate. Structurally, the medulla is comprised of elongate cylindrical cells, to 25 µm diam., with occasional rhizines, to ~8.0 µm diam., and a 2-cell layered cortex. Cystocarps, 200–500 µm diam., project strongly and are centrally situated in terminal branchlets. Spherical to oval tetrasporangia, 25–30 µm diam. and 34–39 µm long, are located in sub-spatulate branchlets. Algae are reddish brown in color.

Habitat and Comments: In Puerto Rico, *Pterocladiella capillacea* occurs intertidally in wave-exposed habitats, extending to 8.0 m depths. [Additional illustrations: Huisman et al. 2007: 111; Littler et al. 2008: 102; Braune and Guiry 2011: fig. 118.1.]

Gigartinales F.Schmitz

Caulacanthaceae Kütz.

Catenella Grev.

Catenella Grev. 1830: LXXVII, nom. cons.

Thalli are mostly repent, consisting of terete to compressed axes that reach 2.0–5.0 cm in extent. The axes, attached by lateral haptera, are segmented by constrictions, and branches arise from the distal ends of the elongated internodes. Erect axes are short, 2.0–3.0 cm tall. Axes are hollow, the medulla comprising several longitudinal filaments that give rise to a reticulum of radiating filaments. Outwardly, the cortex consists of anticlinal rows of 2–5 cells. The life history involves an alternation of isomorphic generations. Gametophytes are dioecious. Spermatangia are cut off from outer cortical cells and occur as scattered clusters. Carpogonial branches are 2– or 3–(5)-celled, and gonimoblasts develop inwardly. The carposporophytes are borne on short, thickened segments. Zonately divided tetrasporangia are scattered within branchlet cortical layers. There is one *Catenella* species in Puerto Rico of the five species known worldwide.

Catenella caespitosa (With.) L.M.Irvine

FIGURE 62

Catenella caespitosa (With.) L.M.Irvine in Parke and Dixon 1976: 590.

Basionym: *Ulva caespitosa* With. 1776: 735.

Heterotypic Synonym: Catenella repens (Lightf.) Batters 1902: 69.

Puerto Rican Records: As *Catenella caespitosa*: Ballantine and Aponte 1997a, 2002a. As *Catenella repens*: Almodóvar and Biebl 1962; Almodóvar 1965; Almodóvar and Pagán 1971 (as *Catenella* sp.); Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Belize, United States (Florida), Bermuda, Bahamas, Cuba, Guadeloupe, Jamaica, Martinique, Panama, Puerto Rico, Tortola, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela, Argentina.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Anglesey, Wales.

Thalli mostly repent, axes are dorsiventrally compressed and divided into segments by regular constrictions. Thalli creep over the substratum with assurgent branches and are anchored by abundant rhizoidal haptera. Oval to spindle-shaped segments are 0.2–0.5 cm in diameter and 0.6–3.0 cm in length. Branching occurs from the constricted nodes and is di- or trichotomous. Structurally, the medulla is composed of thick-walled cells that form a loose network. The 2–3- layered cortex is composed of small compact cells. Gametangial thalli produce fertile lateral branchlets. Spermatangia occur in small protuberances on the fertile laterals. Carposporophytes, 200–300 µm diam., occur terminally on the fertile laterals. Ovoid tetrasporangia, 50–60(–80) µm diam., are scattered among outer cells of the cortex. Algae are dull purple in color.

FIGURE 62. *Catenella caespitosa*. DLB5391, herbarium specimen, Leeward Guayacan Island, epiphytic on *Rhizophora*, 0.5 m. Scale bar = 1.0 cm.

Habitat and Comments: In Puerto Rico, *Catenella caespitosa* is mostly found as an intertidal epiphyte on mangrove prop roots and on other substrata in intertidal sheltered locales. Prud'homme van Rein et al. (1983) detailed reproduction for the species in culture on the basis of Dutch material. [Additional illustrations: Taylor 1960: pl. 66: fig. 13; Aung 2018: figs. 2–11.]

Cystocloniaceae Kütz.

Calliblepharis Kütz.

Calliblepharis Kütz. 1843: 403, nom. cons.

Uniaxial thalli are flattened to compressed and are to 30 cm in length. Most species are anchored by a characteristic fibrous base. The medulla is pseudoparenchymatous, possessing a distinct central axial filament. Carposporangia form in chains, terminally on gonimoblast filaments. Tetrasporangia occur in proliferous branchlets. Eleven species of *Calliblepharis* are recognized, one of which occurs in Puerto Rico.

Calliblepharis saidana (Holmes) M.Y.Yang et M.S.Kim

Calliblepharis saidana (Holmes) M.Y.Yang et M.S.Kim 2017: 93, figs. 1–4.

Basionym: *Hypnea saidana* Holmes 1896: 256, pl. 11: fig. 3a,b.

Heterotypic Synonym: Hypnea volubilis Searles in Schneider and Searles 1976: 53.

Puerto Rican Records (as *Hypnea volubilis*): Ballantine and Aponte 1997a, 1997b; Ballantine and Aponte 2002a; Ballantine et al. 2016b.

Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina, South Carolina, Florida), Puerto Rico, Brazil.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Enoshima, Japan.

Thalli are largely repent, reaching up to 4.0–6.0 cm in extent. Attachment is by marginal rhizoidal pads and by rhizoids issued from branch tips. Flattened axes, 600–750 µm thick and 0.4–0.9(–2.0) mm broad, are irregularly to subdichotomously branched in one plane. Ultimate branchlets measure 160–330 µm diam. and 1.0–6.0 mm long. Structurally, there is a central axial cell surrounded by medullary cells that grade to smaller cells outwardly. There is no sharp distinction between the medulla and the cortex. Surface cortical cells are isodiametric, measuring 6.0–48 µm diam. Spermatangia occur in elevated sori as well as simply scattered over surface cells. Cystocarps are borne laterally on first-order branches and are nearly spherical in shape, 350 µm diam. Tetrasporangia, 17–24 µm diam. and 25–42 µm long, occur in slightly elevated sori in middle to distal regions of the first-order branches. Algae are rose red in color.

Habitat and Comments: *Calliblepharis saidana* in Puerto Rico is somewhat smaller, to 2.0 cm in height and to 0.5 mm in width, than the dimensions given in the account of Searles in Schneider and Searles (1976). All of the Puerto Rican specimens were obtained by dredging at 17–60 m depths. Campbell et al. (2022), on the bases of morphological and genetic examination, found that topotype material from North Carolina was conspecific with *Calliblepharis saidana*. [Illustrations: as *Hypnea volubilis*, Schneider and Searles 1976: figs. 3, 4, 6–10; Ballantine and Aponte 1997b: figs. 5, 6; as *Calliblepharis saidana*, Campbell et al. 2022: figs. 5–9.]

Hypnea J.V.Lamour.

Hypnea J.V.Lamour. 1813: 131.

Uniaxial thalli with prominent apical cells are terete or compressed. Thalli are erect or occur in entangled clumps. Branching is irregular, and thalli frequently possess short spinelike laterals. In sectional view, axes are pseudoparenchymatous. Gametophytes and tetrasporophytes are morphologically identical. Spermatangia are arranged in clusters. Female gametophytes possess 3-celled carpogonial branches, and auxiliary cells are intercalary. Cystocarps protrude from female thalli, and gonimoblasts possess a single terminal carposporangia. Zonately divided tetrasporangia occur in nemathecia or sori. Five of the 63 recognized species of *Hypnea* occur in Puerto Rico.

Comments: Crypsis is increasingly being recognized among *Hypnea* species, with newly added species recognized on genetic bases in the warm temperate and tropical western Atlantic region (Nauer et al. 2015, 2019, 2024; Cabrera et al. 2020).

KEY TO THE *HYPNEA* AND *CALLIBLEPHARIS* SPECIES OF PUERTO RICO

1. Axes bearing stellate propagules. . . . . ***H. cornuta***
   Axes not bearing stellate propagules 2
2. Branches terminating in thickened crozier tips . . . . . ***H. musciformis***
   Branches not terminating in thickened crozier tips 3
3. Thallus axes flattened. . . . . ***C. saidana***
   Thallus axes not flattened. 4
4. Thalli with distinct main axis and rare branch anastomoses. . . . . ***H. cervicornis***
   Thalli without distinct main axes and abundant branch anastomoses . . . . . ***H. spinella***

Hypnea cervicornis J.Agardh

Hypnea cervicornis J.Agardh 1851: 451–452.

Puerto Rican Records: Díaz-Piferrer 1963; Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar 1965; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine et al. 1987.

Western Atlantic Distribution: Belize, Caribbean Mexico, Panama, United States (North Carolina, Florida), Barbados, Cayman Islands, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Barthélemy, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Bahia State, Brazil, fide Haroun and Prud'homme van Reine (1993).

Thalli are generally entangled with primary axes to 15 cm in length. Firm or cartilaginous axes, 0.4–1.0 mm diam., are attached by a primary discoid holdfast in addition to secondary holdfasts issued from branches. Wide-angled branching is of 3 or 4 orders and is subdichotomous to alternate, sometimes cervicorn. Occasionally, branches may anastomose. Spinelike branchlets, 90–170 µm diam. and 160–960 µm long, are scattered on axes. Structurally, there is a 1–2-layered medulla of thick-walled cells, 100–320 µm diam., and a 1–2-layered cortex of round

or elongate pigmented cells, 5.0–10 µm diam. and 7.0–12 µm long. Lenticular thickenings are common in medullary cells. Cystocarps are borne on slender, acute branchlets. Tetrasporangia occur in sori and measure 17–27 µm diam. and 30–52 µm long. Algae are reddish in color.

Habitat and Comments: *Hypnea cervicornis* is common in shallow-water environments. Thalli in wave-exposed habitats tend to be compact, and those from protected habitats tend to be more lax. Lawson and John (1987: 238) wrote, "There is much confusion regarding the distinction between *Hypnea cervicornis* and *H. spinella* taxonomically, nomenclaturally, and biologically." Børgesen (1920) speculated that *H. spinella* might be a dwarf form of *H. cervicornis*, and Silva et al. (1996) and Xia and Zhang (1999) treated *H. spinella* as a synonym of *Hypnea cervicornis*. However, Nauer et al. (2014) considered the two to be distinct species on the basis of molecular and morphological characters. The newly described *Hypnea spiniformis* Nauer, Freshwater et M.T.Fujii from Florida was reported as being morphologically similar to *H. cervicornis* while genetically divergent for COI-5P and *rbc*L genetic markers. This conclusion was also accepted by Wynne (2017) and Guiry and Guiry (2024). [Illustrations: Xia and Wang 1997: figs. 6–10; Cordeiro-Marino 1978: figs. 185–188; Barreto de Jesus et al. 2014: fig. 3A–K; Nauer et al. 2014: figs. 23–32.]

Hypnea cornuta (Kütz.) J.Agardh

FIGURE 63

Hypnea cornuta (Kütz.) J.Agardh 1851: 449.

Basionym: Chondroclonium cornutum Kütz. 1849: 741.

Misapplied Name: Hypnea valentiae (Turner) Mont. 1840: 161 [Montagne 1840].

Puerto Rican Records: As *Hypnea cornuta*: Díaz-Piferrer 1963; Almodóvar 1964a, 1965; Almodóvar and Ballantine 1983. As *Hypnea valentiae*: Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Belize, North America, Bermuda, Cuba, Guadeloupe, Hispaniola, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: "Ad oras Guineae" fide Agardh 1851.

Thalli reach up to 20(–40) cm in height. Terete principal axes, 0.4–1.5 mm diam., are alternately branched. Numerous spinose branchlets, ~2.2 mm long, occur on the axes. Axes also produce numerous sessile or pedicellate stellate branchlets (propagules) with 3–6 apices. Structurally, there is a central axis surrounded by thick-walled medullary cells, 50–300 µm diam. Surrounding the medulla is a 1–2-layered cortex of rounded cells, 7.5–12 µm diam. Gametophytes are dioecious. Projecting cystocarps, 325–500 µm diam., produce carposporangia, 5.0–10 µm diam. Oval tetrasporangia, 15–25 µm diam. and 40–50 µm long, are located in the spinelike branchlets.

Habitat and Comments: *Hypnea cornuta* has been regularly collected at the Media Luna algal plain. Propagules released by mature *H. cornuta* readily germinate in culture media (Ballantine, unpublished). There has been some confusion in reference to reports of *H. cornuta* and *H. valentiae* in Puerto Rico and the Caribbean, with the two showing overlap of vegetative characters. Barreto de Jesus et al. (2014) differentiated them on the presence of starlike propagules in the former and absence in the latter. On this basis, all Puerto Rican reports should be of *Hypnea cornuta*. Additionally, by this criterion, Littler and Littler's (2000) report of *H. valentiae* should also be considered *H. cornuta*. Barreto de Jesus et al. (2019) subsequently reported that some Brazilian specimens referred to *H. cornuta* were a new cryptic species that they described as *H. cryptica* Barreto de Jesus et J.M.C.Nunes and concluded both *H. cornuta* and *H. cryptica* occur in Brazil. Cabrera et al. (2020) recently reported *H. cryptica* in Cuba. *Hypnea cryptica* lacks the stellate propagules that are present in Puerto Rican *H. cornuta*. [Additional illustrations: as *Hypnea cornuta*, Littler et al. 2008: 104; Barreto de Jesus et al. 2014: fig. 6A–I; as *Hypnea valentiae*, Won et al. 2010: figs. 34–36.]

Hypnea musciformis (Wulfen) J.V.Lamour.

FIGURE 64

Hypnea musciformis (Wulfen) J.V.Lamour. 1813: 43.

Basionym: *Fucus musciformis* Wulfen in Jacquin 1791: 154, pl. 14: fig. 3.

Puerto Rican Records: Hauck 1888; Almodóvar and Blomquist 1959, 1961; Taylor 1960; Almodóvar and Biebl 1962; Almodóvar 1964a, 1964b; Díaz-Piferrer and Caballer de Pérez 1964; Schwartz and Almodóvar 1971; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Belize, Costa Rica, Panama, Caribbean Mexico, United States (Connecticut, Virginia, North Carolina, South Carolina, Georgia, Florida), Bermuda, Bahamas, Cayman Islands, Cuba, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela, Uruguay.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Trieste, Italy.

Hypnea musciformis is the type species of the genus. Thalli are bushy and frequently entangled. Primary erect axes, 1.0–2.0 mm diam., reach to 10–20(–50) cm in height and are irregularly or alternately branched to several orders. The axes possess abundant short straight or curved spur-like branchlets, 1.0–5.0(–10) mm long, and acute branch tips are frequently swollen and hooked. The crozier-like hooked apices bear small branchlets dorsally. Structurally, there is a central axial cell surrounded by a medulla of 3–4 layers of thick-walled cells, 40–300 µm diam. The pigmented cortical cells, 7.0–18 µm diam., are in 2 rows. Swollen cystocarps, 0.3–1.0 mm diam.,

FIGURE 63. *Hypnea cornuta*. DLB3341, herbarium specimen, algal plain, 1.5 km seaward Media Luna Reef, 17 m. Habit of specimen. Scale bar = 2.0 cm. Inset: Close-up of an asexual propagule; scale bar = 0.5 mm.

FIGURE 64. *Hypnea musciformis*. DLBsn, herbarium specimen, Ballena Bay, Guánica, 1.0–2.0 m. Scale bar = 2.0 cm.

are clustered in branchlets. Pyriform carposporangia measure 19–30 µm diam. and 20–45 µm long. Ovoid tetrasporangia, 22–30 µm diam. and 40–85 µm long, are cut off by cortical cells and are located in spindle-shaped branchlets. Algae are dull purplish red, sometimes greenish in color.

Habitat and Comments: *Hypnea musciformis* is found in both wave-exposed and protected habitats, to 26 m depth. Thalli are epilithic or epiphytic, and the species is commonly adrift in shallow-water back-reef environments. It can attach to seagrasses or other algae by means of entwining at its crozier tips. Nauer et al. (2015, 2019) segregated three additional species from *Hypnea musciformis* in the Caribbean: *H. pseudomusciformis* Nauer, Cassano et M.C.Oliveira (known from Brazil and Uruguay), *H. caraibica* Nauer, Cassano et M.C.Olivera (known from Jamaica and the Dominican Republic), and *H. schneideri* Nauer, Cassano et M.C.Olivera (known from the Dominican Republic). Substantial morphological overlap exists among these species (see Nauer et al. 2019: table I), and these species are principally delimited molecularly. Nauer et al. (2015, 2019) also claimed that species that have been referred to *H. musciformis* also include *H. nigrescens* Grev. ex J.Agardh. and *H. valentiae* (Turner) Mont. [Additional illustrations: Cordeiro-Marino 1978: figs. 182–184; Littler et al. 2008: 105; Won et al. 2010: figs. 25–29; Braune and Guiry 2011: fig. 160.2; Barreto de Jesus et al. 2014: fig. 7A–I; Nauer et al. 2014: figs. 33–48.]

Hypnea spinella (C.Agardh) Kütz.

FIGURE 65

Hypnea spinella (C.Agardh) Kütz. 1847: 23.

Basionym: *Sphaerococcus spinellus* C.Agardh 1822: 323.

Heterotypic Synonym: *Hypnea musciformis* f. *spinella* Hauck 1888: 463.

Puerto Rican Records: As *Hypnea spinella*: Almodóvar 1962, 1964a, 1964b, 1971; Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar and Pagán 1971; Schwartz and Almodóvar 1971; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a. As *Hypnea musciformis* f. *spinella*: Hauck 1988.

Western Atlantic Distribution: Belize, Costa Rica, Caribbean Mexico, United States (Florida), Bermuda, Bahamas, Cuba, Grenada, Hispaniola, Martinique, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: West Indies.

Thalli form entangled, spreading mats to 2.5 cm thick or not matted and reaching up to 15 cm in height. Axes possess frequent anastomoses. Thalli are attached by discoid holdfasts and secondarily by rhizoidal pads from decumbent branches. Cylindrical principal axes, 0.4–1.0 mm diam., are subdichotomously branched below and alternately branched above. Ultimate branches, 90–150 µm diam. and 130–440 µm long, are spinelike. Structurally, the medulla has a conspicuous axial cell surrounded by 1–2 layers of thick-walled medullary cells, 100–300 µm diam.

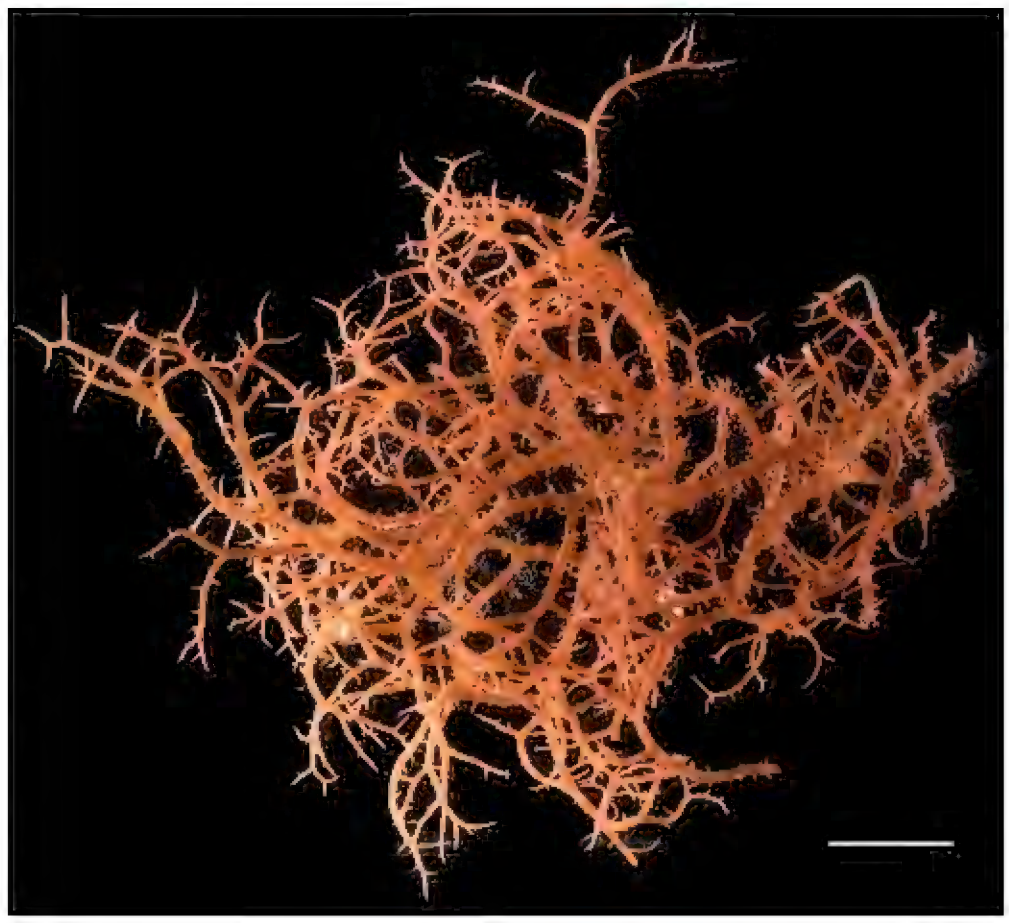

FIGURE 65. *Hypnea spinella*. DLB8257, Laurel Reef, 0.5 m. Scale bar = 1.9 cm.

The cortex consists of 1–2 layers of rounded cells, 7.5–25 µm diam. Gametophytes are dioecious. Hemispherical cystocarps, 0.1–0.9 mm diam., are protruding, and carposporangia measure 5.0–12 µm diam. Ovoid tetrasporangia, 10–25 µm diam. and 40–50 µm long, occur toward the center of the ultimate branchlets. Algae are pale to dark red in color.

Habitat and Comments: *Hypnea spinella* is frequently encountered in shallow, exposed localities, extending to mid-depth environments. [Additional illustrations: Cordeiro-Marino 1978: figs. 179–181; Littler et al. 2008: 106; Won et al. 2010: figs. 30–33; Braune and Guiry 2011: fig. 160.4; Barreto de Jesus et al. 2014: fig. 13A–G.]

Excluded Taxon

Hypnea krugiana **Hauck 1888: 463.**

Taylor (1960) treated *Hypnea krugiana* as a doubtful record, speculating that the specimens could be *H. spinella*. Since Hauck's (1888) publication based on collection in Manati, Puerto Rico, there have been no further reports of *H. krugiana* in Puerto Rico or elsewhere; thus, it cannot be confirmed for Puerto Rico.

Hypneocolax Børgesen

Hypneocolax Børgesen 1920: 479.

Thalli, considered to be parasitic on *Hypnea* species, possess endophytic filaments that emerge to form small pustules.

Structurally, thalli are pseudoparenchymatous, with a medulla of larger cells and a cortex of smaller cells in anticlinal series. Pigmentation is normally reduced or not present; however, thalli have been reported as being pigmented. Spermatangia occur in patches that nearly cover the entire thallus. Cystocarps are immersed and without pores. Tetrasporophytes typically give rise to bisporangia and tetrasporangia that are cut off by cortical cells. *Hypneocolax* is monotypic.

Hypneocolax stellaris Børgesen

FIGURE 66

Hypneocolax stellaris Børgesen 1920: 479.

Puerto Rican Records: Ballantine et al. 2009.

Western Atlantic Distribution: Caribbean Mexico. United States (Florida), Puerto Rico, U.S. Virgin Islands, Colombia.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Lime Tree Bay, St. Croix, U.S. Virgin Islands.

Hypneocolax stellaris is the generitype of the genus. Thalli are wartlike or stellate, ~750 µm wide, with rounded or acute apices. The algae are considered to be parasitic on species of *Hypnea* and develop from its endophytic filaments that emerge from within the infected host. Thalli possess a thick cuticle, 20–25 µm, and barely penetrate the host tissue. Structurally, thalli are pseudoparenchymatous, with a medulla of larger cells and a cortex of smaller cells in anticlinal series. Pigmentation is normally reduced or not present; however, some pustules have been reported as being pigmented. Carpospores measure 20–22 µm diam. Tetrasporophytes typically produce bisporangia, 16–22 µm diam. and 30 µm long, and tetrasporangia. Algae are whitish to pinkish in color.

Habitat and Comments: *Hypneocolax stellaris* is rare in Puerto Rico, having been collected only from the algal plain offshore from Media Luna reef, where it was an epiphyte/parasite on *Hypnea spinella*. [Additional illustrations: Børgesen 1920: figs. 433–435; Huisman et al. 2007: 89.]

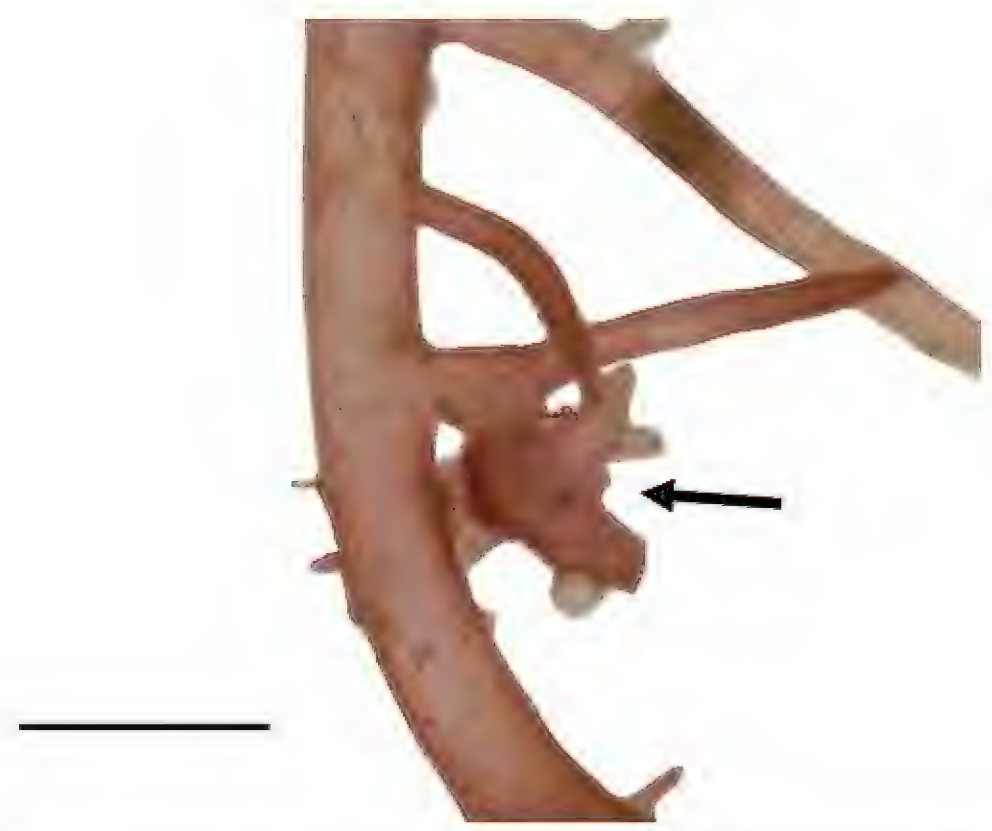

FIGURE 66. *Hypneocolax stellaris*. DLB6932, seaward Media Luna algal plain, 17 m. The parasite (arrow) is growing epiphytically on *Hypnea spinella*. Scale bar = 1.0 mm.

Dumontiaceae Bory

Dudresnaya P.Crouan et H.Crouan

Dudresnaya P.Crouan et H.Crouan 1835: 98, nom. et typ. cons.

Thalli are generally soft and mucilaginous, with cylindrical to complanate axes that are radially alternate or irregularly branched to 2–4 orders. Structurally, thalli are uniaxial; however, the medulla is composed of many longitudinal filaments. Axial cells give rise to 2–7 cortical fascicles of sub-ditrichotomously branched filaments. Cortical filaments are composed of subcylindrical or subspherical uninucleate cells. In some species, axial cells contain crystalline inclusions. Rhizoidal filaments, cut off from proximal cortical fascicle cells, surround the axial medulla. Reproduction involves either an isomorphic or heteromorphic alternation of generations. Gametophytes are monoecious or dioecious. Spermatangia occur in terminal clusters on distal cells of cortical fascicles. Carpogonia are terminal on distally recurved carpogonial branch filaments. Auxiliary cells are intercalary on separate filaments. Fertilized carpogonia divide and fuse with 1 or more cells of the carpogonial branch. Connecting filaments issuing from the fusion, contact, and diploidize auxiliary cells. Gonimoblasts originate from the connecting filament in contact with an auxiliary cell, resulting in a cystocarp that lacks a pericarp. Tetrasporangia are zonately divided when there is an isomorphic alternation of generations or cruciately divided when the alternation of generations is heteromorphic. Tetrasporangia are borne terminally on cortical filaments. Two of the 23 recognized *Dudresnaya* species occur in Puerto Rico.

KEY TO THE *DUDRESNAYA* SPECIES OF PUERTO RICO

1. Distal portion of cortical filaments cylindrical, axial cells possessing hexagonal crystal inclusions . . . . . .*D. crassa*
   Distal portion of filaments ellipsoidal; axial cells possessing rectangular crystal inclusions . . . . . *D. puertoricensis*

Dudresnaya crassa M.Howe

FIGURE 67

Dudresnaya crassa M.Howe 1905: 572, pl. XXVIII, pl. XXIX: figs. 12–26.

Puerto Rican Records: Almodóvar 1970; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Belize, Caribbean Mexico, United States (North Carolina, Florida), Bermuda, Puerto Rico, Brazil, Colombia.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Bermuda.

Thalli are densely branched and very lubricous, reaching up to 5.0–25 cm tall. Main axes measure 5.0–10 mm diam., and the terminal branchlets are ~1.0 mm diam. Axial filaments measure 50–165 µm diam. and 200–430 µm long. Cortical fascicles, 4–6 times dichotomously branched, are cut off in whorls of 4, below the distal end of the bearing axial cell. Cells of the cortical filaments, 3.0–4.6 µm diam., decrease in diameter distally. Hexagonal crystalline inclusions are present within axial cells. Gametophytes are dioecious. Cylindrical to ovoid spermatangia, 2.0–3.0 µm diam., are terminal on cortical filaments. Carpogonial branches are 6–10 cells long. The auxiliary cell is a relatively small cell toward the middle of the auxiliary cell branch. Mature cystocarps measure 130–165 µm diam., and ovoid carposporangia measure 7.0–15 µm diam. Zonately divided tetrasporangia, 10–13 µm diam., occur terminally on cortical branch cells. Algae are rose red in color.

Habitat and Comments: *Dudresnaya crassa* is common in Puerto Rico, particularly at 17 m depth at the Media Luna algal plain. [Additional illustrations: Guimarães and Amado-Filho 2008: figs. 10–17.]

Dudresnaya puertoricensis Searles et D.L.Ballant.

FIGURE 68

Dudresnaya puertoricensis Searles et D.L.Ballant. 1986: 389, figs. 1–24.

Puerto Rican Records: Searles and Ballantine 1986; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, United States (Georgia), Puerto Rico, Colombia.

Type Locality: Offshore from Pitahaya, La Parguera, southwest Puerto Rico.

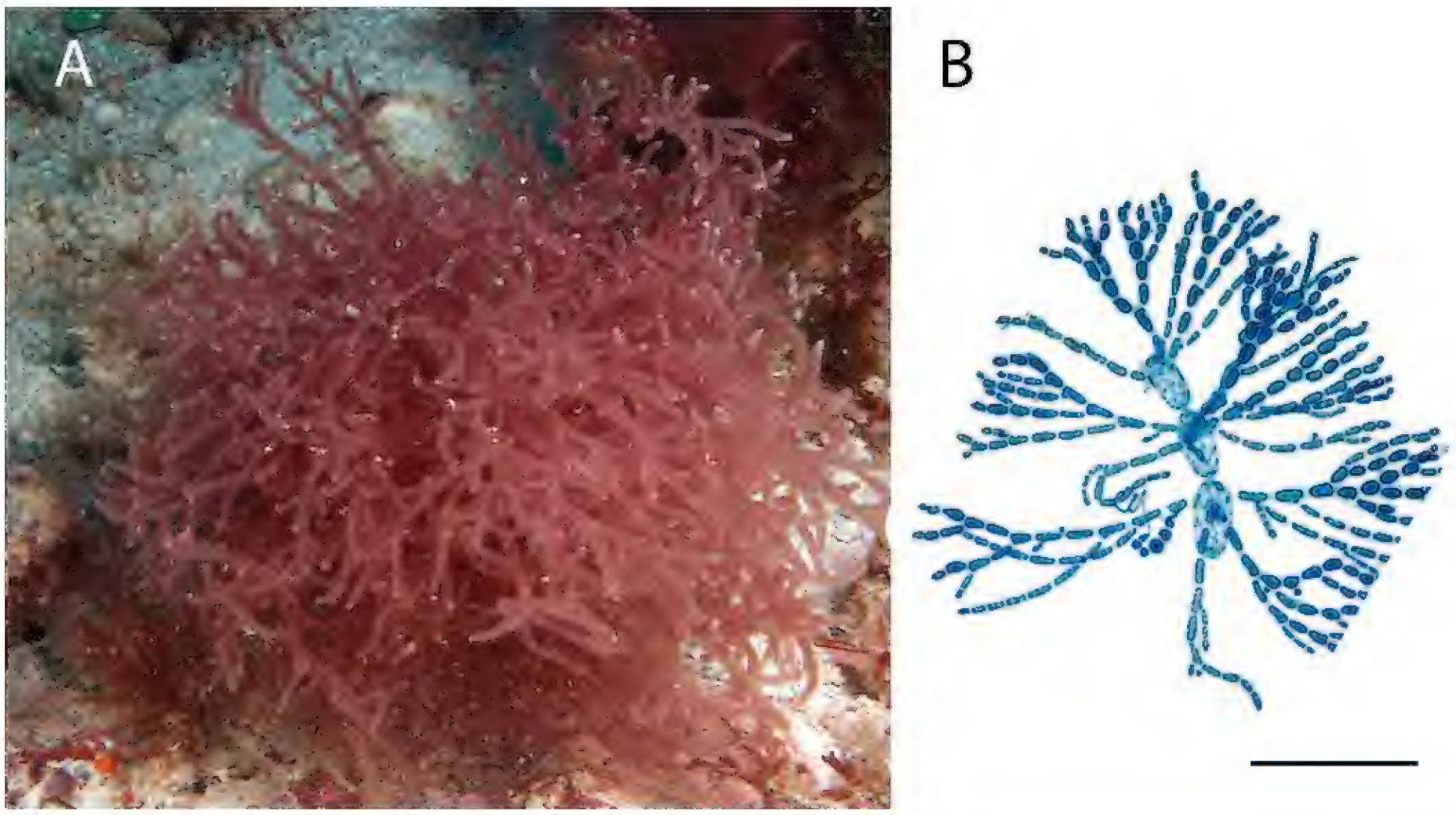

FIGURE 67. *Dudresnaya crassa*. (A) In situ habit photograph, 1.5 km seaward Media Luna Reef, 17 m, La Parguera. Field is approximately 25 cm. (B) DLB6799, photomicrograph showing cortical fascicle with 6-celled recurved carpogonial branch bearing a spiraled trichogyne. Scale bar = 500 µm.

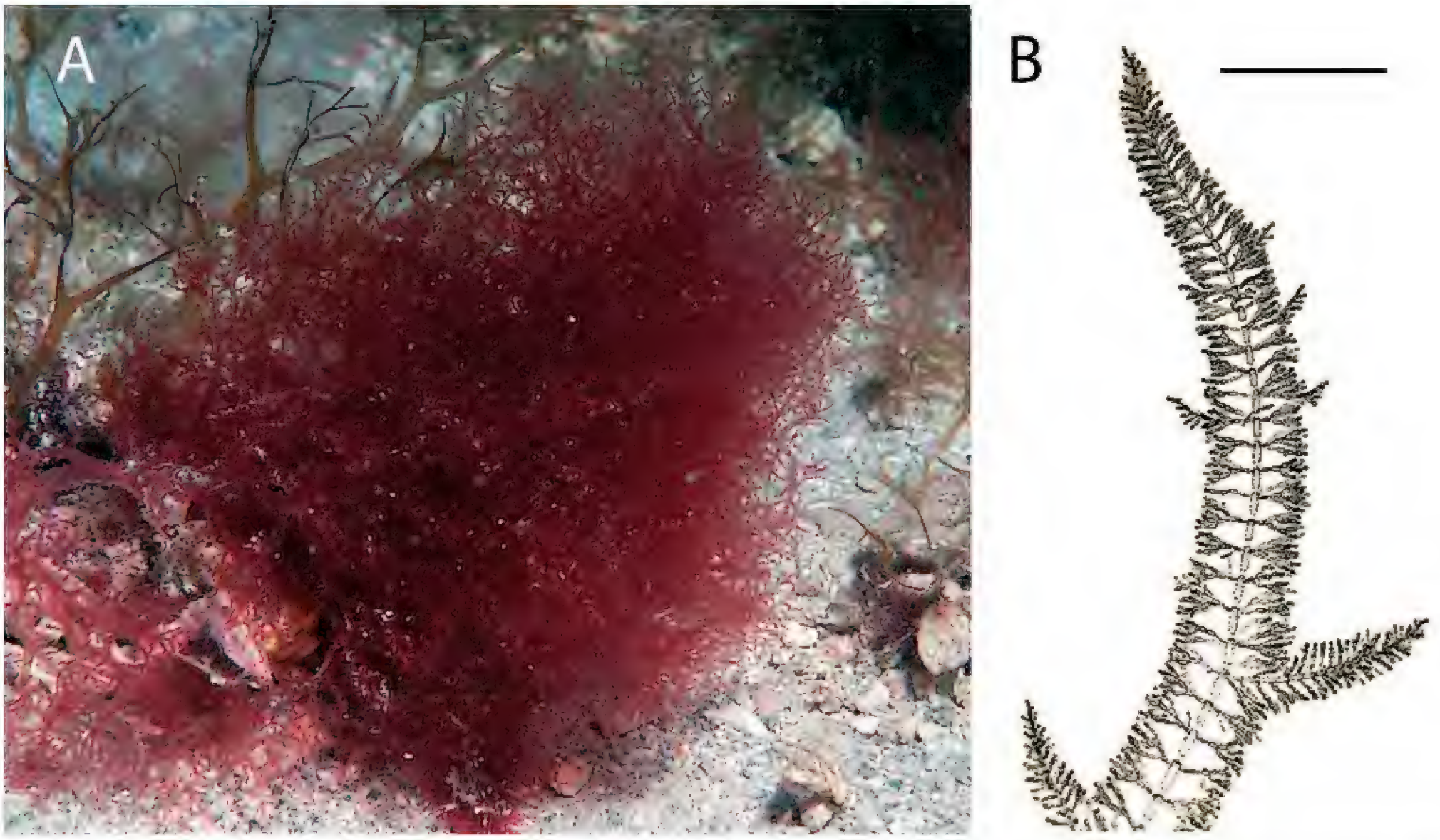

FIGURE 68. *Dudresnaya puertoricensis*. (A) In situ habit photograph, 1.5 km seaward Media Luna Reef, 17 m. Field is approximately 10 cm. (B) DLB6799B, photomicrograph showing arrangement of determinate branchlets and indeterminate branches. Note exserted apical cell. Scale bar = 250 µm.

Thalli of generally terete, abundantly branched axes are to 8.0 cm in height and to 1.3 mm diam. Apical cells of indeterminate branches are distinct and exserted. Axial cells are elongate, to 700 µm diam. and 600–700 µm long. Mature axial cells possess rectangular crystals, 7.0 µm wide and 25 µm long. Four determinate branches are formed around each axial cell. Proximal cortical cells are elongate, and distal cells are ellipsoidal. Inner cells of the cortical fascicle often bear distinctive lateral globose or pyriform cells. Gametophytes are monecious. Ovoid to spherical, to 3.0 µm diam., spermatangia occur on terminal or subterminal cells of the cortical branches. Carpogonial and auxiliary cell branches are located on inner cortical cells. Carpogonial branches are 7–9 cells long. Following presumed fertilization, the carpogonium forms a connecting filament that fuses with the third and fourth cells below the carpogonium. Up to three connecting filaments are then formed. Auxiliary cell branches are up to 12 cells long with a deeply staining auxiliary cell, 2–5 cells from the base of the branch. The subspherical carposporophyte measures to 140 µm diam. Carposporangia are to 9.0 µm diam. Tetrasporophytes are unknown.

Habitat and Comments: *Dudresnaya puertoricensis* grows epiphytically or epilithically. The species has only occasionally been collected at the Media Luna algal plain.

Etheliaceae K.R.Dixon, C.W.Schneid. et G.W.Saunders

Ethelia (Weber Bosse) Weber Bosse

Ethelia (Weber-Bosse) Weber-Bosse 1921: 297.

Noncalcified thalli are crustose and attached across the entire ventral surface by rhizoids or by peg-like outgrowths. The crusts display uniaxial growth and possess a mesothallus or internal veins that give rise to radiating cortical cell filaments that produce both a perithallus inferior and a perithallus superior. Presumed tetrasporangia occur terminally on dorsal cortical filaments. Gametophytes are unknown. Of the 11 *Ethelia* species recognized worldwide, 2 of them are known from Puerto Rico.

KEY TO THE *ETHELIA* SPECIES OF PUERTO RICO

1. Crusts are bright orange, 1.0–3.0 mm thick; primary axial cell to 140 µm diam. . . . . *E. crassa*
   Crusts are dull orange, to 1.0 mm thick; primary axial cell to 70 µm diam. . . . . *E. magnienii*

Ethelia crassa D.L.Ballant., H.Ruiz, Lozada-Troche et J.N.Norris

FIGURE 69

Ethelia crassa D.L.Ballant., H.Ruiz, Lozada-Troche et J.N.Norris 2017: 646, figs. 11–18.

Puerto Rican Records: Ballantine et al. 2017.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Entrance to Bahia Sucia, Cabo Rojo lighthouse, Puerto Rico.

Thalli are fleshy cartilaginous crusts affixed to the substratum across the entire ventral surface. The crusts are up to 50 cm in extent and measure 0.8–1.0(–3.0) mm thick. The principal axial cells, 75–145 µm diam. and 50–100 µm long, run parallel to the plane of the substratum. Horizontal filaments are branched and fanlike. The cortical filaments initially run parallel to axial cells prior to arching toward the dorsal or ventral surfaces. Laterally oriented cortical filaments contribute to specimen breadth. Proximal cortical cells average 6.6 µm diam. and are 30–45 µm long. Distal cells of the superior perithallus filaments terminate in a series of 10 to >20 deeply staining, cuboidal to slightly longer than broad cells measuring 8.0–10 µm diam. and 10–18 µm long. Spherical inclusions are prominent in proximal perithallial cells. Ventral perithallial cells terminate in spherical darkly staining, disorganized cells. The ventral cell masses may give rise to short multicellular rhizoids. The superior perithallus is 63%–83% of total thickness of the perithallus. Thalli are bright orange when living.

Habitat and Comments: *Ethelia crassa* is known from a single shallow-water habitat exposed to high wave energy, on rocks at the entrance to Bahia Sucia in southwest Puerto Rico.

Ethelia magnienii D.L.Ballant., H. Ruiz, Lozada-Troche et J.N.Norris

FIGURE 70

Ethelia magnienii D.L.Ballant., H.Ruiz, Lozada-Troche et J.N.Norris 2017: 641, 644, figs. 6–10.

Puerto Rican Records: As *Ethelia* sp.: Ballantine et al. 2016b. As *Ethelia magnienii*: Ballantine et al. 2017.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Edge of insular shelf ("El Hoyo") offshore from La Parguera, Puerto Rico.

Thalli are encrustations that are affixed to the substrata across the entire ventral surface and by peg-like attachment haptera. Darkly staining principal axial filaments, oriented along the

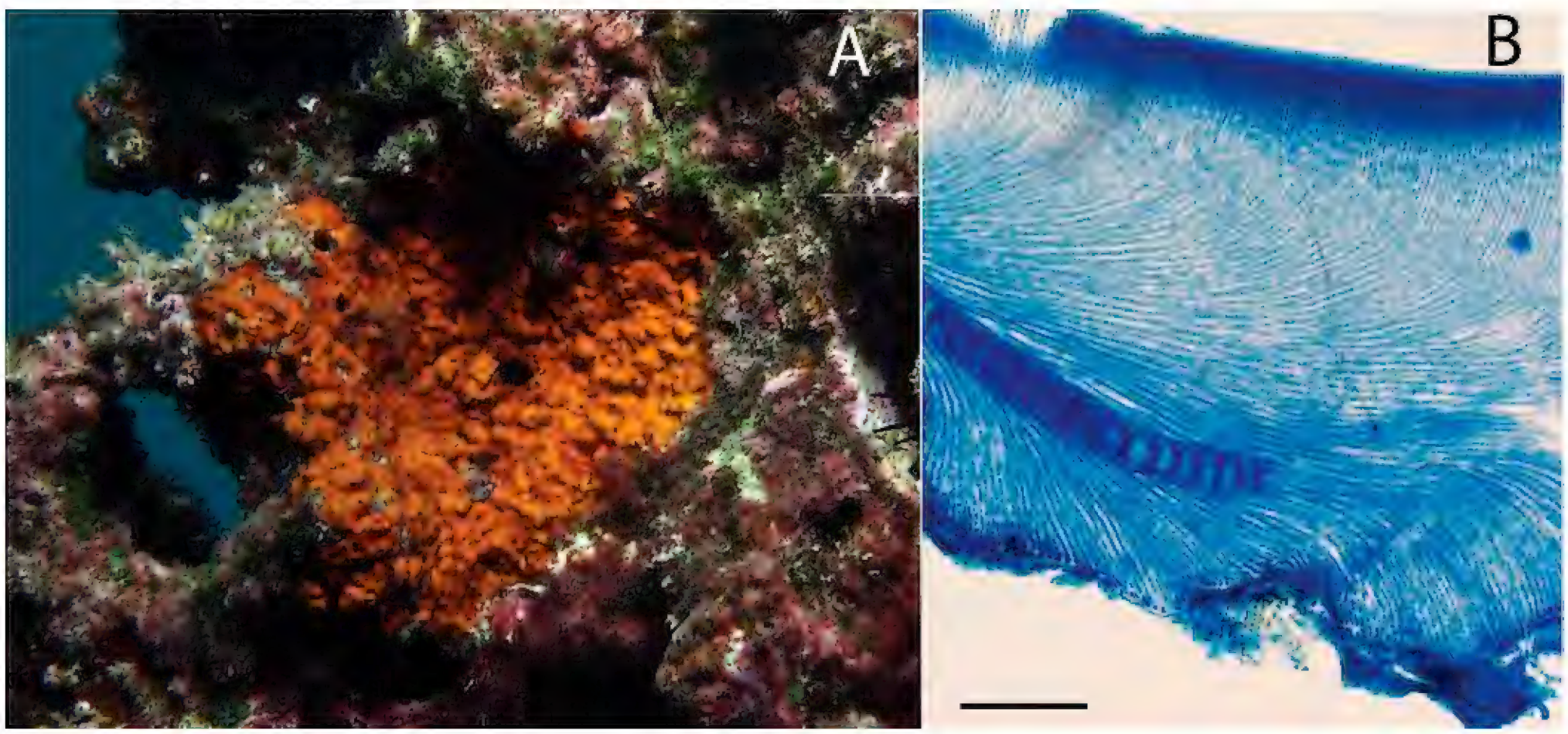

FIGURE 69. *Ethelia crassa*. (A) In situ habit photograph, growing in shallow water on rock outcrop near entrance to Bahia Sucia. Field is approximately 25 cm. (B) DLB8338B, photomicrograph of transverse section showing central axial filament giving rise to superior and inferior perithalli. Scale bar = 100 µm.

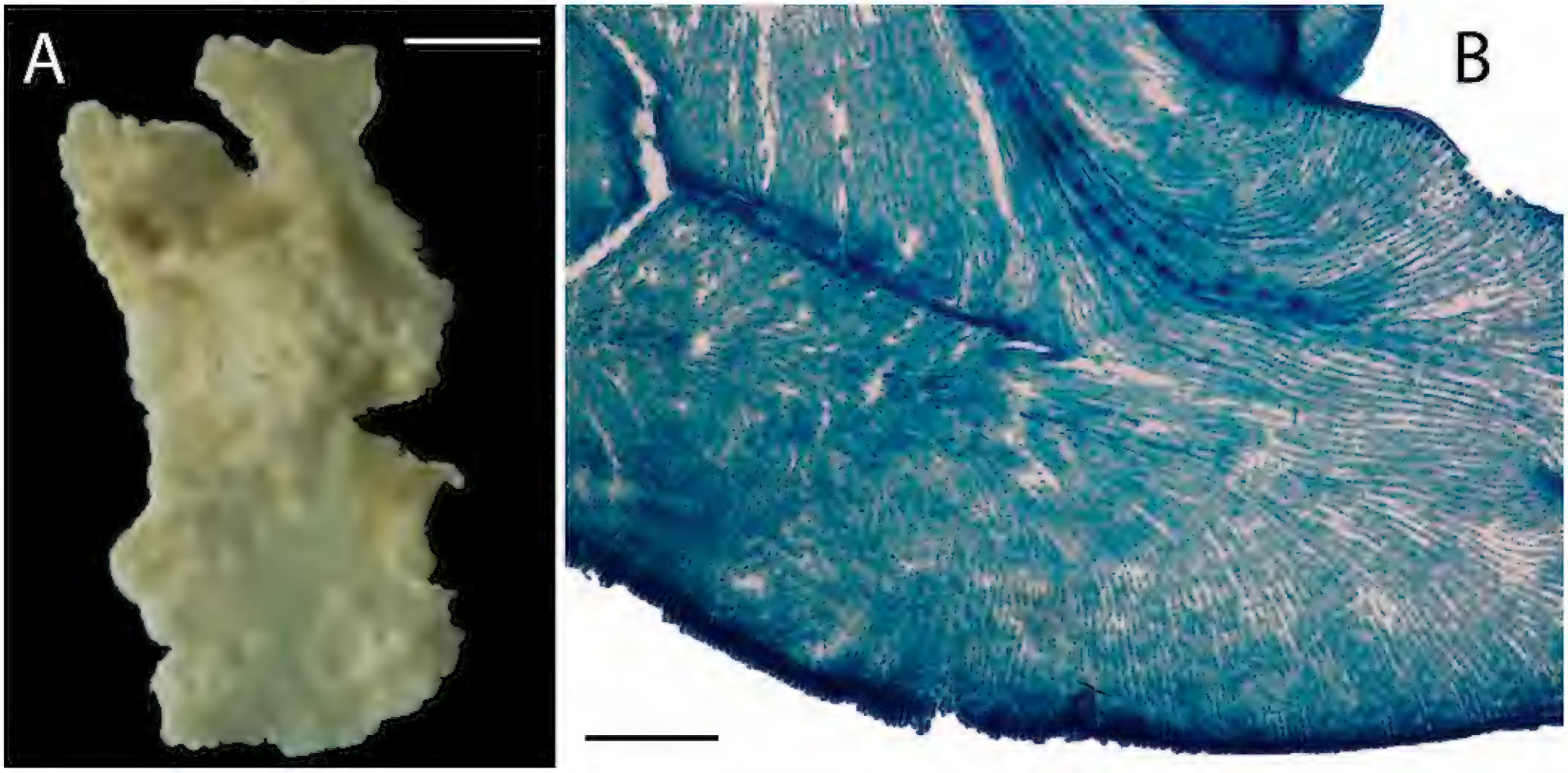

FIGURE 70. *Ethelia magnienii*. (A) DLB7858, holotype specimen, edge of insular shelf offshore from La Parguera, 82 m. Scale bar = 0.5 cm. (B) Transverse section showing central axial filaments giving rise to superior and inferior perithalli. Scale bar = 100 µm.

plane of the substratum, are composed of cells 40–70 µm diam. and 50–65 µm long. These give rise to cortical filaments that initially run parallel to axial cells prior to arching toward the dorsal or ventral surfaces or laterally to contribute to the breadth of the crust. Cortical cells are small, 3.0 µm diam. and 6–7 µm long. Dorsal filaments terminate in 3–4 small cuboidal, darkly staining cells. Ventral filaments terminate in short, somewhat disorganized, irregularly shaped cells. Hollow regions occur irregularly within the crust. Short rhizoids are occasionally cut off by the non-organized ventral cells. The proportion of the superior perithallus to the total perithallus thickness is 50%–70%. Gametophytes and tetrasporophyte structures are unknown. Algae are light orange in color.

Habitat and Comments: Crusts have been exclusively collected in deepwater habitats, greater than 60 m in depth, on the southern Puerto Rican insular shelf.

Kallymeniaceae Kylin

Austrokallymenia Huisman et G.W.Saunders

Austrokallymenia Huisman et G.W.Saunders in Saunders et al. 2017: 100.

Thalli are perforate expanded blades. The medulla possesses branched filaments and stellate cells with elongate arms. The medullary filaments outwardly support a subcortex of 1–2 layers of larger polygonal cells. An outer cortex consists of 2–4 layers of smaller rounded pigmented cells. Reproductively, the genus displays an isomorphic alternation of generations. Spermatangial mother cells are cut off from outer cortical cells. Female gametophytes have polycarpogonial support cells, and following fertilization, a prominent fusion cell is formed. Carposporophytes are embedded within the medulla. Scattered subspherical or ellipsoidal tetrasporangia are cruciately or irregularly zonately divided. Six species of *Austrokallymenia* are recognized; one of these occurs in Puerto Rico.

Austrokallymenia westii (Ganesan) C.W.Schneid. et G.W.Saunders

FIGURE 71

Austrokallymenia westii (Ganesan) C.W.Schneid. et G.W.Saunders in Schneider et al. 2019: 416, fig. 2.

Basionym: *Kallymenia westii* Ganesan 1976: 169, figs. 1–12, 14, 16–21.

Misapplied Name: Kallymenia perforata J.Agardh 1872: 9.

Puerto Rican Records: As *Kallymenia perforata*: Almodóvar and Blomquist 1965; Almodóvar et al. 1979; Almodóvar and Ballantine 1983. As *Kallymenia westii*: Ballantine and Aponte 1997a, 2002a. *As Austrokallymenia westii*: Schneider et al. 2019.

Western Atlantic Distribution: Caribbean Mexico, United States (Texas, North Carolina, Florida), Bermuda, Martinique, Puerto Rico, U.S. Virgin Islands, Colombia, Venezuela.

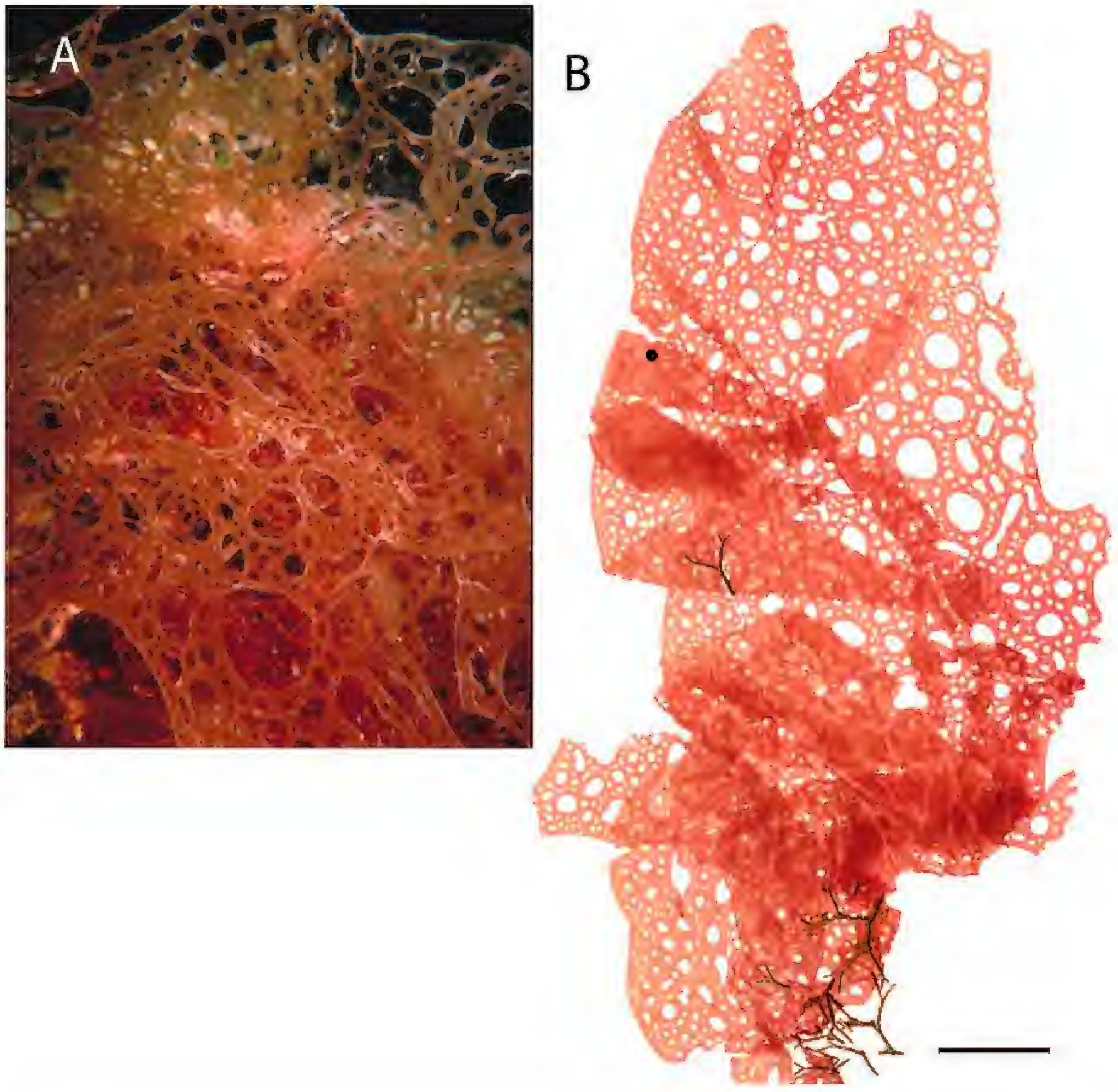

FIGURE 71. *Austrokallymenia westii*. (A) In situ photograph, seaward Margarita Reef, 24 m. (B) DLBsn, herbarium specimen, algal plain, seaward Margarita Reef, 24 m. Scale bar = 2.0 cm.

World Distribution: See Guiry and Guiry 2024.
Type Locality: El Farallon, Isla de Margarita, Venezuela.

Thalli form large orbicular or lobed blades, 10–50(–100) cm in extent. The blades, 200–500 µm thick, are perforate and gelatinous in texture. Perforations are smaller in young blades and larger, 1.0–2.5 cm diam., in older blades. The medulla consists of filaments, 4.0–6.0(–20) µm diam., and stellate ganglia, 60–90 µm diam. The 1–2-layered inner cortex cells measure 15–90 µm diam. Surface cortical cells are 3.0–12 µm diam. Spherical carposporophytes measure 0.5–1.0 mm diam. Ovoid tetrasporangia, 10–15 µm diam. and 12–25 µm long, are scattered in the cortex. Algae are red to pale pink in color.

Habitat and Comments: *Austrokallymenia westii* is relatively rare in Puerto Rico; most collections have been at the Margarita algal plain at 24 m depth. Schneider et al. (2019) transferred North Carolina, Bermuda, and U.S. Virgin Islands specimens referred to *Kallymenia westii* to *Austrokallymenia*. *Austrokallymenia* was segregated from *Kallymenia* principally on the basis of *rbc*L sequence analyses (Saunders et al. 2017). [Additional illustrations: Littler and Littler 2000: 81.]

Meredithia J.Agardh

Meredithia J.Agardh 1892: 73.

Thalli are semi-peltate blades, borne on terete perennial stipes. The medulla consists of compact filaments with stellate cells and a cortex of subspherical cells. Reproductively, the genus displays a heteromorphic alternation of generations with dioecious procarpic gametophytes. Carpogonial branches are 3-celled and are borne singly on elongate supporting cells on medullary filaments. Cystocarps become projecting with maturation. Spermatangia occur in sori. Tetrasporophytes are crustose with zonate tetrasporangia. Until the publication of Schneider et al. (2014), *Meredithia* was considered to be monotypic and restricted to the eastern Atlantic and Mediterranean. They added 7 new species, including one from Bermuda in the west Atlantic, *M. crenata* C.W.Schneid., G.W.Saunders et C.E.Lane. There are 2 *Meredithia* species in Puerto Rico, and 12 species are recognized worldwide.

KEY TO THE *MEREDITHIA* SPECIES OF PUERTO RICO

1. Thalli sprawling, producing new blades from the parent blade margin. . . . . ***M. caribaea***
   Mature thalli entirely erect, primary axis serially giving rise to new irregularly circular blades . . . . . ***M. pulchella***

Meredithia? caribaea D.L.Ballant, H.Ruiz et J.N.Norris

FIGURE 72

Meredithia? caribaea D.L.Ballant, H.Ruiz et J.N.Norris 2015: 356, figs. 5–7.
Puerto Rican Records: Ballantine et al. 2015, 2016b.
Western Atlantic Distribution: Puerto Rico.
Type Locality: Edge of insular shelf, La Parguera, Puerto Rico.

Immature thalli are reniform to nearly circular and concave or shallowly cuplike peltate blades. Algae are attached to the substratum by short, occasionally branched, central, or submarginal stipes, up to 2.0 mm long. The blades, to 11 mm diam. and 115 µm thick, possess crenate margins. New blades are formed by lobes from the parent blade margin or from new stipes produced dorsally from parent blades; the laterally coherent blades are repent and spreading and measure to 5.0 cm in extent. Medullary filaments measure to 4.0 µm in diameter, and stellate ganglia are occasionally present within the medulla. The colorless medullary filaments connect to the inner cortical cells. The cortex of both surfaces are mostly 3(–4) cell layers, with the inner cortical cells up to 23 µm in largest dimension and the cortical cells outwardly decreasing to 5.0 µm diam. toward the surface. No reproduction was observed.

Habitat and Comments: A taxonomic query was given to generic placement of the species, *Meredithia? caribaea*. Although its reproduction was unknown, it was otherwise in agreement with the morphology of the genus (Ballantine et al. 2015). *Meredithia? caribaea* is known from two deepwater collections to 70 m as well as from the Media Luna algal plain at 17 m. The species may be distinguished from all other species of the genus, with the exception of *M. crenata* and *M. pulchella* (below), by its distinctive dentate-erose margins.

FIGURE 72. *Meredithia? caribaea*. DLB7947 (top) and DLB8492, holotype (bottom), Turrumote Reef. Scale bar = 2.0 cm. Illustration by Alice Tangerini.

Meredithia pulchella D.L.Ballant, H.Ruiz et J.N.Norris

FIGURE 73

Meredithia pulchella D.L.Ballant, H.Ruiz et J.N.Norris 2015: 358, fig. 8.
Misapplied Name: *Kallymenia limminghei* Mont.
Puerto Rican Records: As *Meredithia pulchella*: Ballantine et al. 2015, 2016b. As *Kallymenia limminghei*: Almodóvar 1971; Ballantine et al. 2011.
Western Atlantic Distribution: Puerto Rico.
Type Locality: Edge of insular shelf, La Parguera, Puerto Rico.

Thalli are up to 3.0 cm in height and possess several serially produced peltate blades. The axis initially gives rise to a peltate irregularly circular blade, which then continues growth via production of a new stipe, generally offset from the position of the lower original stipe, which in turn then develops subsequent

FIGURE 73. *Meredithia pulchella*. DLB7308, habit of the holotype, wet preserved specimen, edge of insular shelf, off La Parguera, 50 m. Scale bar = 1.00 cm.

rounded peltate branches. Blades are flattened to shallowly cup-shaped with crenate margins, to 110 µm thick, with a cortex of 2–3 cell layers. The medulla is composed of thin filaments measuring to 2.0 µm diam. and possesses stellate ganglia. Many of the specimens collected in Puerto Rican possess only 1 or 2 peltate branches.

Habitat and Comments: *Meredithia pulchella* is uncommon in Puerto Rice, being known from deepwater habitats, 50–70 m depths.

PHYLLOPHORACEAE WILLKOMM

Gymnogongrus Mart.

Gymnogongrus Mart. 1833: 27.

Thalli are up to 25 cm in height, arising from crustose bases. Gametophytic thalli are erect, with terete, compressed, or flattened axes. Branching is irregular or dichotomous, sometimes with a proliferation of branchlets. The pseudoparenchymatous medulla is composed of large and small cells. Gametophytes are dioecious. Spermatangia occur in superficial sori, and carposporophytes are immersed but appear as swollen protrusions on the surface. Tetrasporophytic thalli occur as microthallus crusts, or tetrasporangia occur in nemathecia as carpotetrasporangia borne on gametophytes. Thirty-one species of *Gymnogongrus* are recognized, one of which occurs in Puerto Rico.

Gymnogongrus tenuis J.Agardh

FIGURE 74

Gymnogongrus tenuis J.Agardh 1849: 88.

Puerto Rican Records: Díaz-Piferrer 1963; Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

FIGURE 74. *Gymnogongrus tenuis*. DLBsn, herbarium specimen, Ponce, intertidal. Scale bar = 1.0 cm.

Western Atlantic Distribution: Caribbean Mexico, Barbados, Cuba, Dominica, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: West Indies.

Thalli, 2.0–6.0 cm tall, are bushy in appearance. The axes are cartilaginous in texture and flat, 2.0–3.0 mm broad. Branching is dichotomous, becoming polychotomous distally. In section, the medulla is parenchymatous with the largest cells, ~40–50 µm diam. Cells decrease in diameter outwardly. The cortex possesses a thick cuticle. Projecting round to oval cystocarps, ~1.0 mm diam., occur in the central and upper portions. Algae are dull purple in color.

Habitat and Comments: *Gymnogongrus tenuis* is found growing on rocks exposed to the surf, particularly on the north coast. [Additional illustrations: Børgesen 1919: fig. 352; Taylor 1960: pl. 60: fig. 2.]

RHIZOPHYLLIDACEAE ARDISSONE

Contarinia Zanardini

Contarinia Zanardini 1843: 45.

Thalli are noncalcified prostrate flattened blades that are attached by simple multicellular rhizoids. Structurally, thalli are either uniaxial or multiaxial, with a horizontally growing mesothallus that gives rise to assurgent dorsal and ventral perithallial

filaments. The mesothallus may be located centrally or toward the ventral surface. Vesicular cells may occur on dorsal and ventral perithallial filaments. Where known, spermatangial axes form nemathecia. Carpogonial branches and 3- or 4-celled auxiliary cell branches are produced in female nemathecia. Irregularly cruciate or irregularly zonate tetrasporangia are located in nemathecia devoid of paraphyses. Eight species of *Contarinia* are recognized, of which two occur in Puerto Rico.

KEY TO THE *CONTARINIA* SPECIES OF PUERTO RICO

1. Thalli with a central mesothallus ..... *C. ruizii*
   Thalli with the mesothallus situated ventrally ..... *C. pedrochei*

Contarinia pedrochei D.L.Ballant. et H. Ruiz sp. nov.

FIGURE 75

Contarinia pedrochei D.L.Ballant. et H.Ruiz sp. nov., Fig. 75A–D.

Holotype: DLB7892, edge of insular shelf ("Hole in the Wall"), La Parguera (17°53.077′N, 67°1.315′W), Coll. HR, 55 m, 11.xi.2009 (US Alg. Coll. 238305).

Isotypes: US Alg. Coll. 328445–328448.

Paratypes: DLB7444, edge of insular shelf ("Black Wall"), La Parguera (17°53.090′N, 67°00.863′W), Coll. HR, 57 m, 11.xi.2009 (US Alg. Coll. 234109); DLB7031, edge of insular shelf ("Buoy"; 17°53.292′N, 66°59.872′W), Coll. HR, 46 m, 28.xii.2006 (US Alg. Coll. 328468); DLB7419, edge of insular shelf ("Hole in the Wall"), La Parguera (17°53.077′N, 67°1.315′W), Coll. HR, 50 m 15.iv.2003 (US Alg. Coll. 328467); DLB7461, 1.5 km seaward Media Luna Reef, offshore from La Parguera (228450), Coll. DLB, HR, 17 m, 7.v.2005 (US Alg. Coll. 328450); DLB7690, edge of insular shelf ("El Hoyo"), La Parguera (17°52.537′N, 67°2.648′W), Coll. HR, 64 m, 17.xii.2008.

Western Atlantic Distribution: Puerto Rico.

Etymology: The species epithet honors our friend and colleague Francisco F. Pedroche.

Description: Algae form prostate, noncalcified multiaxial thalli that are partially free from the substratum (Figure 75A). Thalli are small, lobed blades with entire margins, sometimes anastomosing. Blades measure to 2.0 cm in extent and are 70–175 µm thick. Occasional multicellular rhizoids, up to 13 µm in diameter (Figure 75B,C), are produced from the ventral surface. The mesothallus is located toward the ventral surface of the blade, occurring as parallel files of cells. The mesothallus gives rise to a superior perithallus of arched files of ascending cells, typically ~5 cells long, that makes up most of the breadth of the blade. The proximal 2 periaxial cells, 25–32 µm long and 8.0–10 µm in diameter, are cut of at an approximate 40° angle. Distal to these cells are somewhat smaller, variously shaped cells that ultimately give rise to 1 or 2 layers of cortical cells that measure ~5.0 µm in diameter. The ventral perithallus is not clearly defined and composed of only 1 or 2 cells. Vesicular cells are cut off terminally by dorsal perithallial cells (Figure 75D). These enlarge, to ~37 µm diam., and ultimately become diffuse while becoming surrounded by cells of the perithallus. The space occupied by the vesicular cells eventually becomes cavities (presumably, their contents are discharged from the dorsal surface of the blade). Algae are reddish to pink in color.

Habitat and Comments: *Contarinia pedrochei* has been collected on numerous occasions growing on coral fragments at mesophotic depths (50–80 m) as well as at the Media Luna algal plain at 17 m depth. *Contarinia pedrochei*, *C. okamurae* Segawa (1941), and *C. ventriglandis* K.R.Dixon in Dixon and Huisman (2018) all possess a multiaxial construction. The two latter species also have a Pacific distribution. The new species differs from *C. okamurae* by its substantially thinner blades (70–175 versus 500–1,000 µm thick; Segawa 1941) and from *C. ventriglandis* in lacking ventrally positioned gland cells (Dixon and Huisman 2018).

Contarinia ruizii D.L.Ballant. sp. nov.

FIGURE 76

Contarinia ruizii D.L.Ballant. sp. nov., Fig. 76A–D.

Holotype: DLB6411, Punta Brea, Guánica, Coll. DLB, HR, 17 m, 20.xii.2004 (US Alg. Coll. 328549).

Isotypes: US Alg. Coll. 328550–328552, 328556.

Paratype: DLB6091, Punta Brea, Guánica, Coll. DLB, HR, 17 m, 14.i.2004 (US Alg. Coll. 238304, 238554, 238555, 238557, 238558, 241405.

Western Atlantic Distribution: Puerto Rico.

Etymology: The species epithet honors our friend and contributor Hector Ruiz. Dr. Ruiz, an accomplished scuba and technical diver and skilled technical scientific and underwater photographer, has collected many of the new species and new records of Puerto Rican algae over the past 25 years.

Description: Thalli, growing on coral fragments, consist of loosely adhered narrow blades to 12 cm long, 2.0–5.0 mm wide, and (150–)180–220(–250) µm thick (Figure 76A–D). The blades partially overgrow other blades in an imbricate fashion (Figure 76B). Multicellular rhizoids, cut off from the ventral surface, measure to 15 µm diam. and to 300 µm long. Thalli are uniaxial, with a centrally positioned mesothallus (Figure 76C). Mesothallial cells are elongate and variable in length, measuring 35–65 µm long and 20–25 µm in diameter. Mesothallus cells cut off perithallial initials that are directed toward the apex at shallow angles both ventrally and dorsally (Figure 76C). The dorsal epithallial filaments arch upward such that a 2–3-layered cortex is more or less perpendicular to the dorsal surface. Proximal

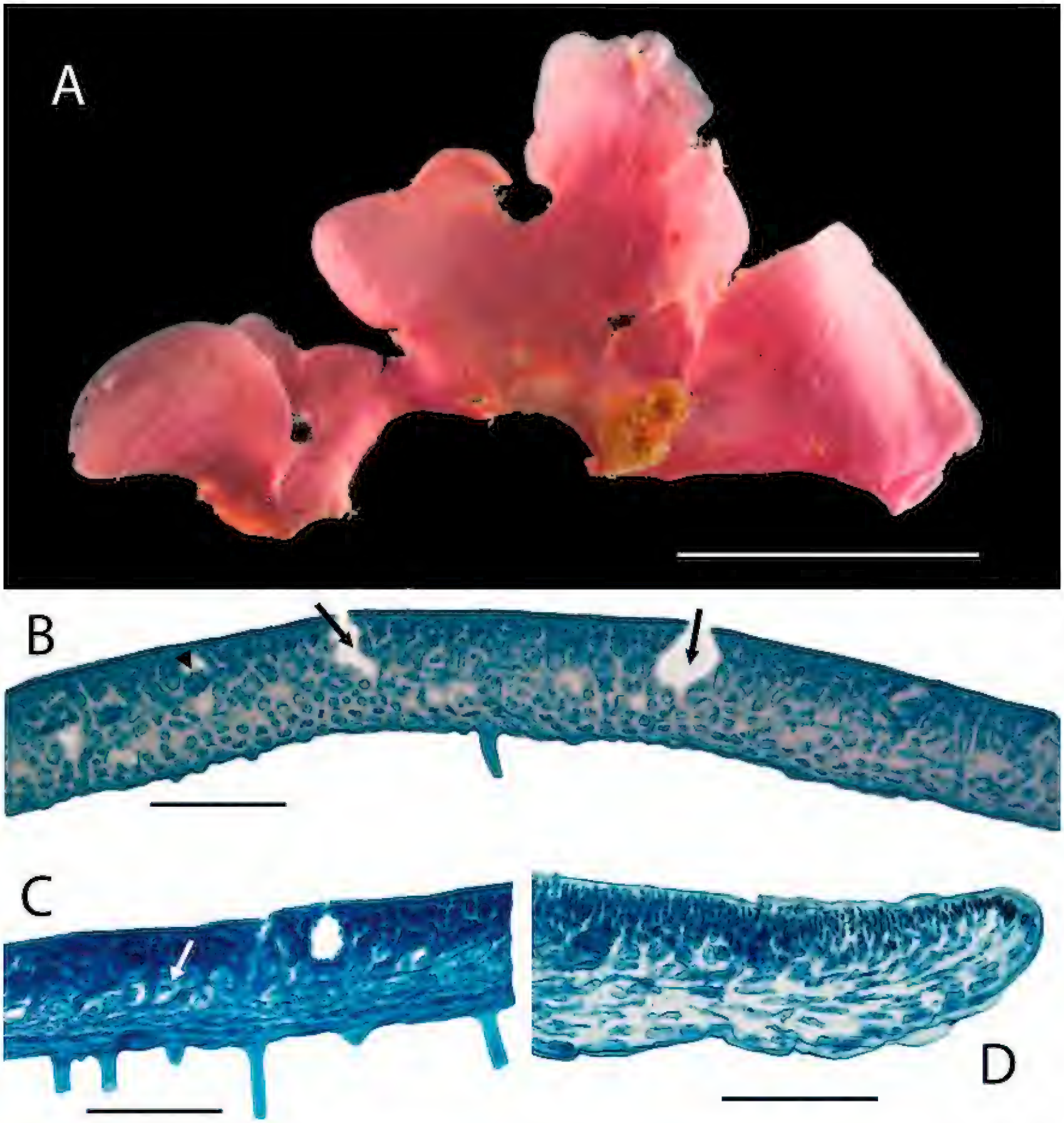

FIGURE 75. *Contarinia pedrochei*. DLB7892. (A) Holotype specimen, edge of insular shelf, 55 m. Scale bar = 1.0 cm. (B) Photomicrograph of tangential section showing gland cells (arrowhead) and empty spaces once occupied by gland cells (arrows). Scale bar = 200 µm. (C) Photomicrograph of radial transverse section showing multiple axial cells running parallel to dorsal portion of thallus. Note also gland cells (arrow). Scale bar = 200 µm. (D) Photomicrograph of radial transverse section at growing margin. Scale bar = 100 µm.

dorsal perithallial cells average 38 µm long and 20–25 µm in diameter. The distal dorsal epithallial cells are shorter and narrower, with the apical perithallial cells averaging ~7.0 µm in diameter. Proximal ventral perithallial cells measure 25–32 µm long and to 15 µm in diameter. The ventral perithallial cells also decrease in length and diameter, terminating in cells that measure ~7.5 µm in diameter. The ventral perithallial cells intersect the ventral surface at roughly 45° angles. Mesothallial and perithallial cells are conspicuously starch filled. Oval to pyriform-shaped gland cells are present in the dorsal perithallus and measure to 65 µm long (Figure 76D). Reproductive thalli are unknown. Algae are orange, pink, or reddish in color.

Habitat and Comments: *Contarinia ruizii* is only known growing on small rock outcrops at the Punta Brea algal plain

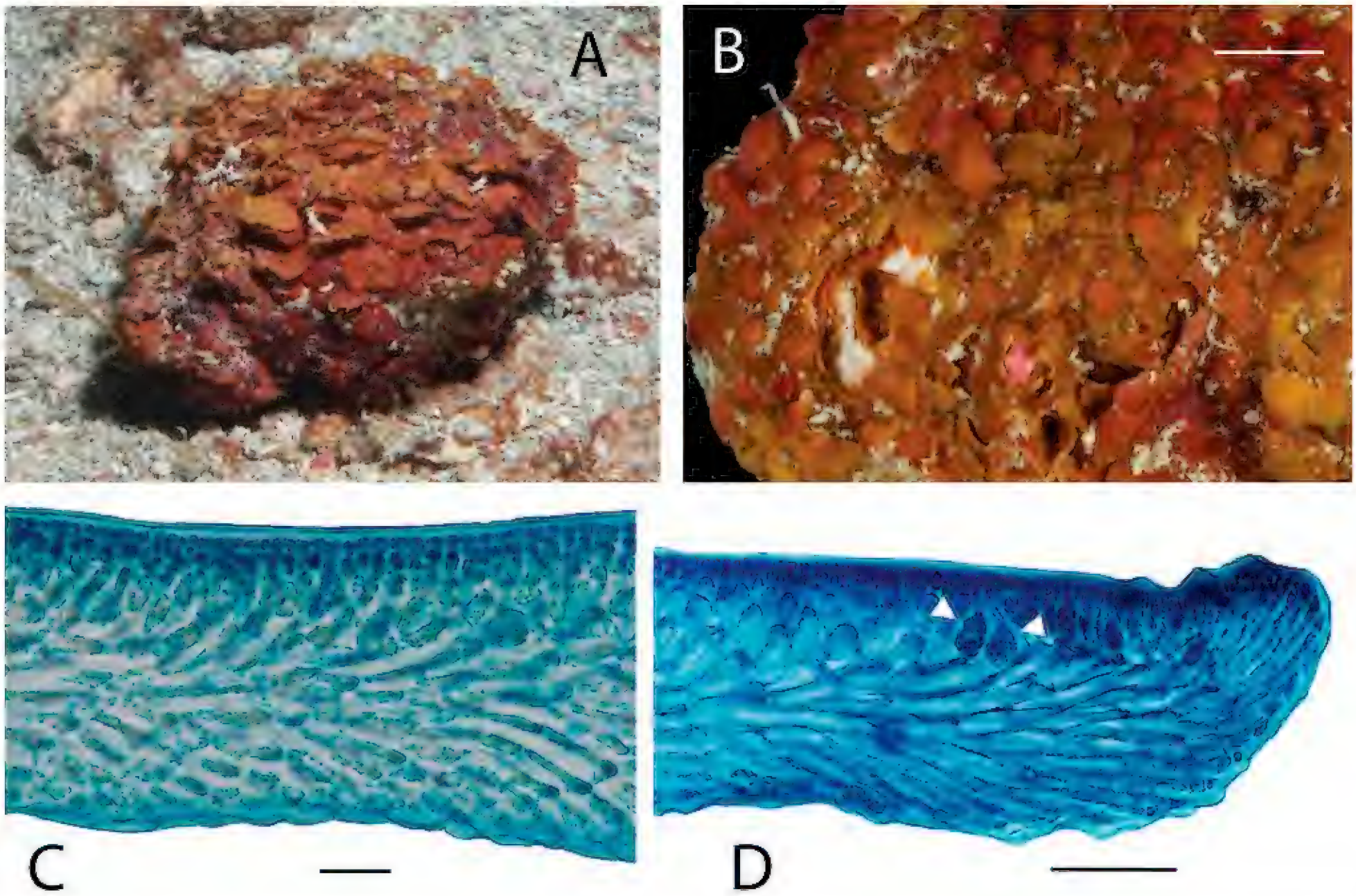

FIGURE 76. *Contarinia ruizii*. DLB6411. (A) In situ photograph of the holotype, algal plain, Punta Bra, Guánica, 17 m. Field is approximately 5.0 cm. (B) Expanded view of the holotype, showing individual bladelets. Scale bar = 0.5 mm. (C) Radial transverse section through holotype specimen, showing uniaxial central mesothallus with cortical filaments cut off apically and dorsally. Scale bar = 50 µm. (D) Radial transverse section through apex; arrowheads denote gland cells. Scale bar = 50 µm.

in southwest Puerto Rico at a depth of 17 m. Prior to the present account, only one *Contarinia* species, *C. magdae* Weber Bosse in Børgesen (1916), was known from the Caribbean region. *Contarinia magdae* is also a uniaxial species, and *C. ruizii* differs in being less than half the thickness of *C. magdae* (180–220 versus 458 µm thick), having evenly developed dorsal and ventral perithalli versus poorly developed ventral perithalli, and not being calcified. Other non-Caribbean uniaxial *Contarinia* species include *C. pacifica* (Børgesen) Denizot (1968), *C. peyssonneliiformis* Zanardini (1843), and *C. squamariae* (Menegh.) Denizot (1968). From the new species, *C. pacifica* also differs in being tightly adherent and in having a less developed ventral perithallus (Børgesen 1924; Dixon and Huisman 2018). *Contarinia peyssonneliiformis* differs in being tightly adherent, having a less developed ventral perithallus and in having perithallial filaments cut off at more less right angles to the axial filament (Peña and Bárbara 2010; Cormaci et al. 2020). *Contarinia squamariae* differs in being tightly attached, possessing a regularly branched habit, as opposed to being unbranched in the new species, and possessing perithallial cells that are cut off at right angles to the axial cell (Denizot 1968; Berecibar et al. 2009). *Contarinia ruizzi* differs from *C. pedrochei* (above) by nature of its uniaxial versus multiaxial construction.

Ochtodes J.Agardh

Ochtodes J.Agardh 1872: 5.

Erect thalli reach to 17 cm in height. Irregularly branched axes are cylindrical and possess 2 apical cells. Gland cells occur in the cortex. Reproductive structures occur in elevated nemathecia. Carpogonial branches are 3–4 cells in length. The lobed carposporophyte possess a protuberant pericarp. Tetrasporangia are zonately to nearly cruciately divided. One of the six recognized *Ochtodes* species is known from Puerto Rico.

Ochtodes secundiramea (Mont.) M.Howe

FIGURE 77

Ochtodes secundiramea (Mont.) M.Howe 1920b: 583.

Basionym: *Hypnea secundiramea* Mont. 1842: 255 [Montagne 1842].

Puerto Rican Records: As *Ochtodes secundiramea*: Howe 1920b; Taylor 1960; Almodóvar 1965; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Panama, Caribbean Mexico, Bahamas, Barbados, Belize, Costa Rica, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Martinique.

Bushy thalli are 4.0–10 cm tall. Cylindrical to slightly compressed axes, ~1.0 mm diam. proximally and decreasing to ~0.1 mm diam. distally, are irregularly or alternately branched, becoming subcorymbose distally. Structurally, the axes possess 2 axial cells, 50–70 µm diam. Surrounding the axial cells is a medulla of 2–3 layers of large colorless cells, 80–100 µm diam., that decrease in diameter outwardly. A cortex of small cells in radial series surrounds the medulla. Surface cortical cells measure ~3.8 µm diam. Numerous elongate gland cells occur in intercalary positions within the radial cortical files of cells. Spermatangia occur in localized nemathecia in distal regions that are ~75 µm thick. Carpogonial branches are borne in nemathecia near the branch tips. Subglobose cystocarps, 450–525 µm diam., are commonly in groups of 2–3. The carpospores measure 4.5–7.6 µm diam. Tetrasporangia, ~8.0 µm diam. and 23 µm long, occur in nemathecia in both proximal and distal thallus portions. Thalli are reddish or reddish purple in color; when iridescent, algae are frequently bluish.

Habitat and Comments: *Ochtodes secundiramea* often occurs in moderately exposed environments in shallow water. [Additional illustrations: Joly and Ugadim 1966: pls. I–III; Littler and Littler 2000: 91.]

FIGURE 77. *Ochtodes secundiramea*. In situ photograph, Sardineras Beach, Isabela, 13 m. Field is approximately 25 cm.

SOLIERIACEAE

Agardhiella F.Schmitz

Agardhiella F.Schmitz in Schmitz and Hauptfleisch 1897: 371.

Thalli, to 30 cm in length, arise from a discoid holdfast. Axes are terete to flattened and irregularly and pinnately or radially branched. Structurally, multiaxial axes possess 4–8 apical cells. The medullary region is hollow, made up of loose to compact interwoven filaments. A cortex of progressively smaller anticlinally oriented cells surrounds the medullary region. Spermatangia, cut off by parent cells in the outer cortex, occur in patches. Carpogonial branches are 3(–4) cells long. Tetrasporangia are cut off laterally from bearing cells and within the cortex. There are two *Agardhiella* species known to Puerto Rico of the five species known worldwide.

KEY TO THE *AGARDHIELLA* SPECIES OF PUERTO RICO

1. Branching radial; axes terete ..... *A. subulata*
   Branching distichous, axes compressed. ..... *A. ramosissima*

Agardhiella ramosissima (Harv.) Kylin

FIGURE 78

Agardhiella ramosissima (Harv.) Kylin 1932: 17.

Basionym: *Chrysymenia ramosissima* Harv. 1853: 190, pl. XXX.B.

Homotypic Synonyms: Neoagarhiella ramosissima (Harv.) M.J.Wynne et W.R.Taylor 1973: 103; *Rhabdonia ramosissima* (Harv.) J.Agardh 1885: 85.

Puerto Rican Records: As *Agardhiella ramosissima*: Taylor 1960; Navarro and Almodóvar 1974; Ballantine and Aponte 1997a, 2002a; Ballantine et al. 2016b. As *Rhabdonia ramosissima*: Hauck 1888. As *Neoagardhiella ramosissima*: Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida, North Carolina), Bermuda, Puerto Rico, U.S. Virgin Islands, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Key West, Florida.

Thalli reach 20–30 cm in height. The fleshy axes are oppositely to irregularly distichously branched to 3–4 orders. The

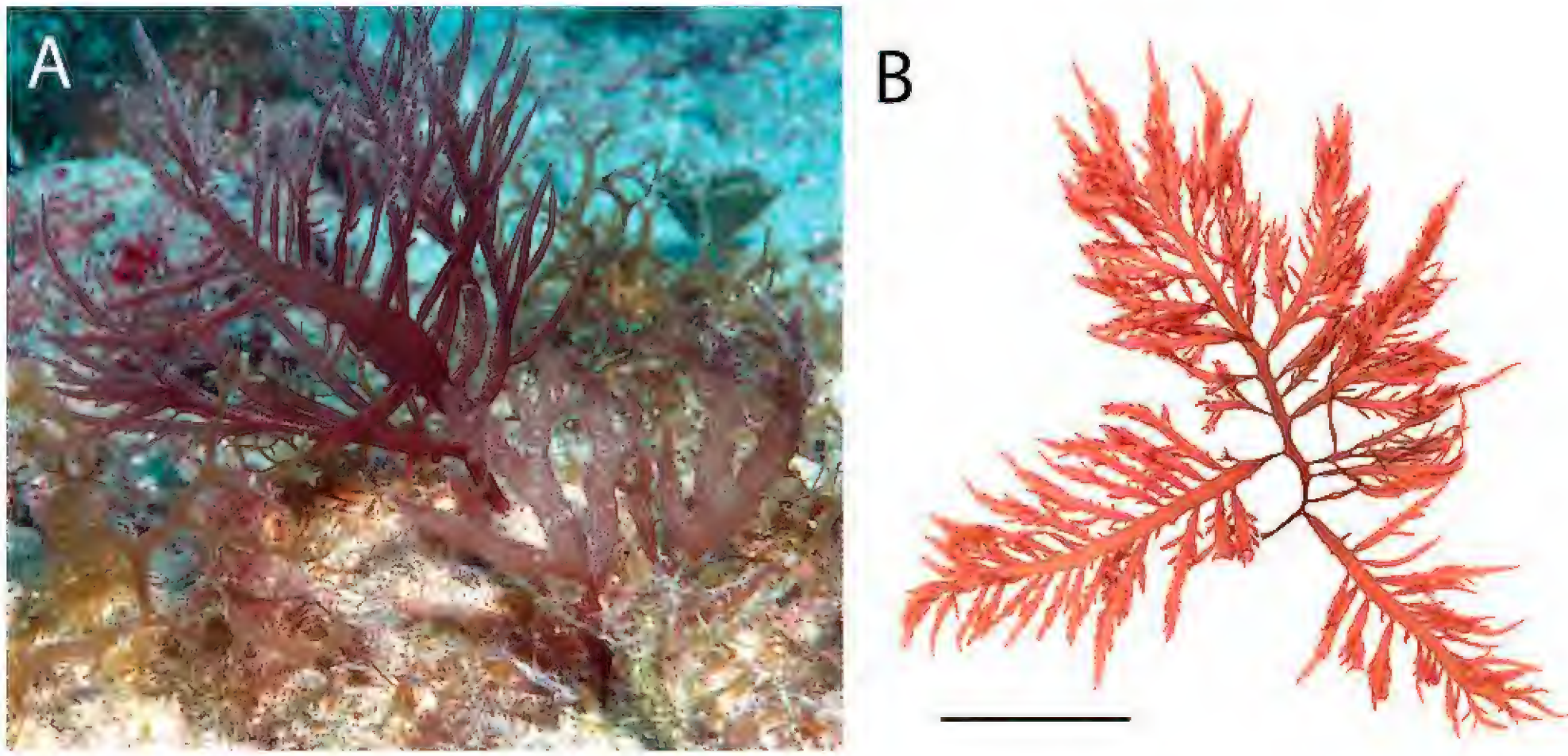

FIGURE 78. *Agardhiella ramosissima*. (A) In situ photograph, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Field = 20 cm. (B) DLB1362, herbarium specimen, algal plain seaward Margarita Reef, 24 m. Scale bar = 5.0 cm.

principal axes are compressed to flattened, 2.0–6.0(–15) cm wide; the ultimate branchlets are terete. Branches are tapered at their origin and taper distally to the acute apices. Entangled medullary filaments measure 2.0–10 µm diam. Surrounding the medulla is an inner cortex of 3–4 layers of cells, 50–250 µm diam., and an outer cortex of 1–2 layers of elongate cells, 7.0–12 µm diam. Gametophytes are dioecious. Spherical carposporophytes, 1.0–1.7 mm diam., are embedded and protrude from the surface of the female thallus. Ovoid carposporangia, 17–38 µm diam. and 20–45 µm long, are borne in terminal chains. Ovoid tetrasporangia measure 30–50 µm diam. and 45–80 µm long. Algae are rose red to brown in color.

Habitat and Comments: *Agardhiella ramosissima* is common in Puerto Rican offshore algal plains, collected to 60 m. [Additional illustrations: Taylor 1960: pl. 58: fig. 5; Littler and Littler 2000: 95.]

Agardhiella subulata (C.Agardh) Kraft et M.J.Wynne

Agardhiella subulata (C.Agardh) Kraft et M.J.Wynne 1979: 329.

Basionym: *Sphaerococcus subulatus* C.Agardh 1822: 328.

Heterotypic Synonym: *Agardhiella tenera* (J.Agardh) F.Schmitz in Schmitz and Hauptfleisch 1897: 371.

Puerto Rican Records: As *Agardhiella subulata*: Ballantine and Aponte 1997a, 2002a. As *Agardhiella tenera*: Taylor 1960; Almodóvar 1964a, 1965; Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida, North Carolina, South Carolina), Bahamas, Barbados, Costa Rica, Cuba, El Salvador, Guadeloupe, Hispaniola, Jamaica, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: "Mari Canadensi."

Thalli are bushy, reaching to about 30(–45) cm in height. Mature thalli possess a fibrous holdfast. The terete axes, 1.0–5.0 mm diam., are 1–3 times alternately radially or somewhat unilaterally branched. Branches are constricted at their bases. Structurally, thalli possess a filamentous medulla, the longitudinal filaments measuring 10–15 µm diam. Surrounding the medulla is a 2–4-layered inner cortex of thick-walled cells, 60–250 µm diam., and a 1–2-layered outer cortex of smaller elongate cells. Gametophytes are dioecious. Spermatangia, 6.0–7.0 µm diam. and 14–17 µm long, are scattered over the surface. Spherical cystocarps, 1.0–2.0 mm diam., give rise to terminal ovoid carposporangia, 15–30 µm diam. and 35–45 µm long. Oval, zonately divided tetrasporangia, 20–45 µm diam. and 44–50 µm long, are situated in the outer cortex. Cystocarps are scattered and only slightly projecting from the surface. Algae are rose red to pinkish in color.

Habitat and Comments: *Agardhiella subulata* grows on rubble and shell fragments in offshore algal plains. Littler et al. (2008) reported the species to 45 m depth. Peterson et al. (2020) pointed out similarities between their new species, *Eucheumatopsis sanibelensis* E.S.Peterson, C.W.Schneid. et G.W.Saunders (2020), and *Agardhiella subulata*. [Illustrations: as *Agardhiella*

tenera, Cordeiro-Marino 1978: figs. 176–178; as *Agardhiella subulata*, Littler and Littler 2008: 109.]

Eucheumatopsis Núñez-Resendiz, Dreckm. et Sentíes

Eucheumatopsis Núñez-Resendiz, Dreckm. et Sentíes in Núñez-Resendiz et al. 2019a.

Erect cartilaginous thalli possess cylindrical axes. Branching is radially alternate, subopposite, or irregular. Axes are multiaxial, with a medulla of thick-walled filaments surrounded by a several-layered cortex of rounded or ovoid cells. The outer cortex is single layered. Gametophytes are dioecious. Cystocarps are located on short laterals and give rise to 2-celled carposporangial chains. Zonately divided tetrasporangia are scattered, cut off from surface cortical cells. One of the two recognized *Eucheumatopsis* species occurs in Puerto Rico.

Note: Núñez-Resendiz et al. (2019a) erected the new genus on the basis of molecular sequence data.

Eucheumatopsis isiformis (C.Agardh) Núñez-Resendiz, Dreckm. et Sentíes

Eucheumatopsis isiformis (C.Agardh) Núñez-Resendiz, Dreckm. et Sentíes 2019a: 55, figs. 3–19.

Basionym: *Sphaerococcus isiformis* C.Agardh 1822: 271.

Homotypic Synonym: Eucheuma isiforme (C.Agardh) J.Agardh 1847: 16.

Puerto Rican Records: As *Eucheuma isiforme*: Almodóvar 1964b; Almodóvar and Ballantine 1983; Cheney 1988; Ballantine and Aponte 1997a, 2002a. As *Eucheumatopsis isiformis*: Núñez-Resendiz et al. 2019a.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Bermuda, Barbados, Belize, Cuba, Guadeloupe, Hispaniola, Puerto Rico, St. Barthélemy, U.S. Virgin Islands.

World Distribution: See Guiry and Guiry 2024.

Type Locality: West Indies, Caribbean Sea.

Eucheumatopsis isiformis is the generitype. Thalli are cartilaginous in texture, reaching 30–70 cm or more in height. Branching is radial to complanate, and there are to 5 orders of branching, although this is highly variable. Axes, 2.0–8.0 mm diam., are terete and frequently spinose (in whorls) or nodulose, sometimes smooth. Structurally, axes possess a medulla of close-packed thick-walled filaments, 3.0–6.0 µm diam., and an inner cortex of large thick-walled cells, 12–80 µm diam., that grades in size to an outer cortex of smaller elongated cells. Cystocarps, 0.5–2.0 mm diam., are hemispherical and located in the branchlets. Ovoid carposporangia measure 9.0–14 µm. Ovoid, zonately divided tetrasporangia, 12–20 µm diam., occur in the outer cortex. Algae are pale straw, yellowish brown or reddish in color.

Habitat and Comments: The species has only rarely been collected in Puerto Rico, and Puerto Rican specimens do not attain the larger dimensions given above. A second species of the genus, *E. sanibelensis* E.S.Peterson, C.W.Schneid. et G.W.Saunders (2020), recently described from the west coast of Florida, is smaller than *E. isiforme* and lacks the ultimate spine-like branchlets of the latter species. [Illustrations: as *Eucheuma isiforme*, Taylor 1960: pl. 45: fig. 11, pl. 50: figs. 6, 7; Dawes et al. 1974: figs. 1–5; Braune and Guiry 2011: fig. 139.1.]

Flahaultia Bornet

Flahaultia Bornet 1892: 279.

Erect thalli develop from a crustose base and reach to 10 cm in length. Flattened multiaxial axes are irregularly branched. The filamentous medulla contains numerous rhizoids. Protruding cystocarps are embedded within the thallus. Carposporangia occur in rows. One of the three recognized *Flahaultia* species occurs in Puerto Rico.

Flahaultia tegetiformans W.R.Taylor

FIGURE 79

Flahaultia tegetiformans W.R.Taylor 1974: 68, figs. 14–24.

Puerto Rican Records: Ballantine and Aponte 1997a, 1997b, 2002a; Ballantine et al. 2016b.

Western Atlantic Distribution: Caribbean Mexico, Cuba, Jamaica, Puerto Rico, St. Eustatius, Colombia.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Sylvia Lawn coral reef, St. Ann Parish, Jamaica.

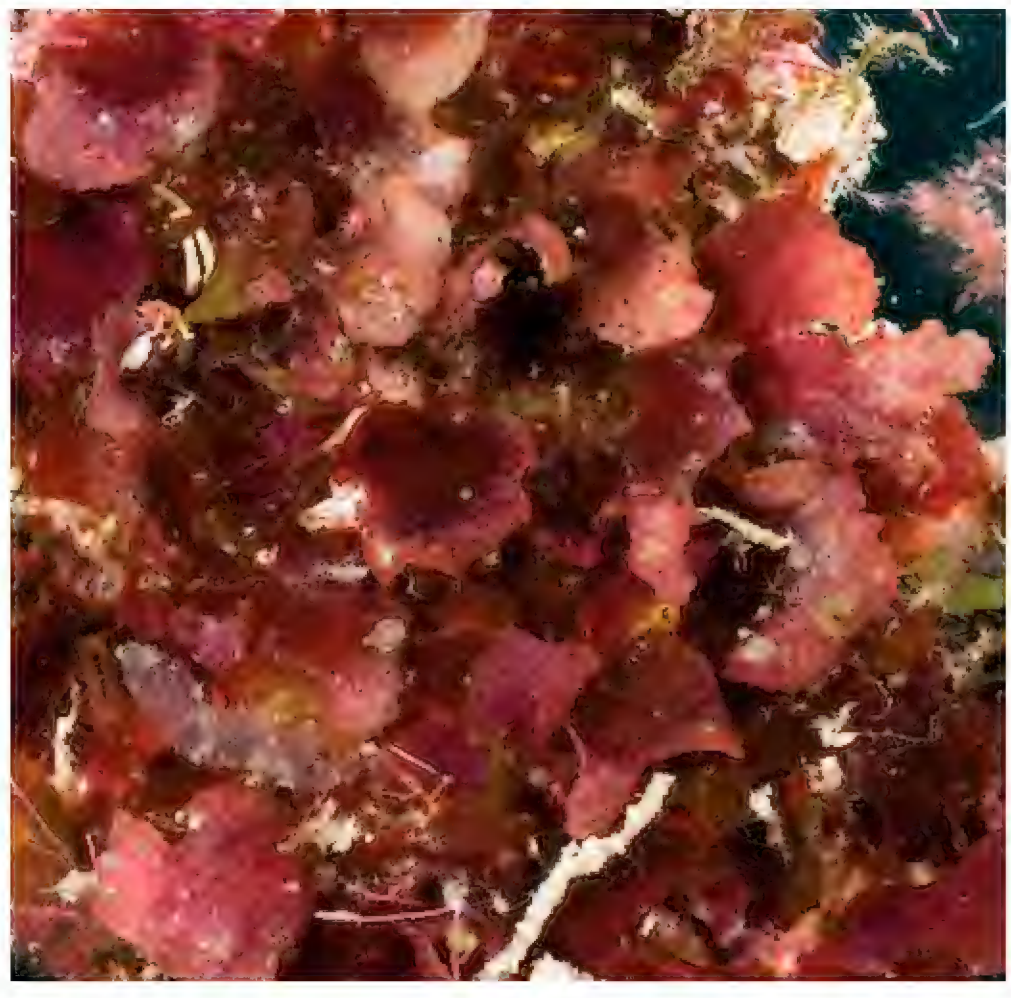

FIGURE 79. *Flahaultia tegetiformans*. Live specimen, edge of insular shelf off La Parguera, 40 m. Field is approximately 5.0 cm.

Thalli are borne on a short, generally marginal or submarginal stipe. Blades, 1.0–4.0 cm wide and 50–165 µm thick, are fan shaped, lobed, and ovate. The blades become proliferous with maturation, becoming decumbent and mat-like and sometimes anastomosing with adjacent blades. The entire thallus reaches to ~15 cm in extent. The medulla consists of dense filaments, 1.5–4.5(–10) µm diam. Surrounding the medulla is a cortex of anticlinal dichotomously branched filaments. The inner cortex is 3-layered, composed of cells, 7.0–11 µm diam., and the outer cortex is composed of cells, 3.0–4.0(–6.0) diam. and 8.0 µm long. Gametophytic and tetrasporophytic thalli are unknown. Algae are red in color.

Habitat and Comments: Taylor (1974) considered the generic assignment of *Flahaultia tegetiformans* to be provisional as reproductive thalli were not found. In Puerto Rico *F. tegetiformans* has been collected only at the edge of the insular shelf off La Parguera growing on the sponge *Verongia* and on coral rubble down to a maximum depth of 61 m. Schneider et al. (2006) discussed the superficial vegetative resemblance of *Flahaultia tegetiformans* to *Crassitegula walsinghamii* G.W.Schneid, C.E.Lane et G.W.Saunders.

Meristotheca J.Agardh

Meristotheca J.Agardh 1872: 37–38.

Erect and decumbent thalli are attached by basal and secondary holdfasts, reaching to 25 cm in height. Axes are terete, compressed, or flattened. Branching is highly varied among species, being radially alternate to irregularly palmate and lobed. Axes are multiaxial and possess a filamentous medulla and a pseudoparenchymatous cortex. Gametophytes are monoecious. Spermatangia form at the surface of carpogonial nemathecia. Inner cortical cells are large and often stellate. Carpogonial branches are 3-celled, and cystocarps are protuberant. Carposporangia are single and terminal. Tetrasporangia, cut off laterally, are zonately divided. Of 13 recognized *Meristotheca* species, 2 occur in Puerto Rico.

KEY TO THE *MERISTOTHECA* SPECIES OF PUERTO RICO

1. Axes terete, 1–5 mm diam., branching alternately opposite, sometimes secund . . . . . ***M. cylindrica***
   Axes compressed to flattened, 3–15 mm broad, branching pinnate, irregular, subdichotomous or palmate . . . . .***M. gelidium***

Meristotheca cylindrica Núñez-Resendiz, Dreckm. et Sentíes

FIGURE 80

Meristotheca cylindrica Núñez-Resendiz, Dreckm. et Sentíes 2017: 424, 425, figs. 2–13.

Puerto Rican Records: Ballantine et al. 2019.

Western Atlantic Distribution: Caribbean Mexico, Puerto Rico.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Bahia Tortuga, Campeche, Mexico.

Thalli reach 5.0 to 32 cm in height. Multiple cartilaginous erect axes originate from a discoid holdfast. The axes are terete to complanate, 1.0–5.0 mm diam. Principal axes are alternately oppositely branched, as are higher orders of branching. There are 2–5 branching orders. Terete branches are thinner, 380–780 µm diam., than the principal axes and possess acute apices. Branch surfaces are mostly smooth, with occasional spine-shaped proliferations that are 1.0–2.5 mm long. Axial filaments, 4.5–7.0 µm diam., cut off periaxial cells that develop into the cortex. A 1–2-layered outer cortex consists of small subspherical to elongate cells, 9.0–15 µm diam. Cystocarpic thalli, 14–16 cm high, are shorter and less branched than tetrasporophytes. Ellipsoidal cystocarps are prominent, 480–672 µm wide and 625–864 µm high, and occur singly or in clusters on branch margins or lateral proliferations. Ellipsoidal tetrasporangia, 18–25 µm wide and 50–60 µm long, are scattered among cortical cells in distal thallus portions. Algae are dark red to violet purple in color.

Habitat and Comments: Puerto Rican specimens of *Meristotheca cylindrica* were exclusively female gametophytes and were collected at 17 m depth at the algal plain offshore from Punta Brea.

Meristotheca gelidium (J.Agardh) E.J.Faye et Masuda

FIGURE 81

Meristotheca gelidium (J.Agardh) E.J.Faye et Masuda: 254 in Faye et al. 2004.

Basionym: *Sphaerococcus gelidium* J.Agardh 1841: 17.

Homotypic Synonyms: Eucheuma gelidium (J.Agardh) J.Agardh 1847: 16; *Meristiella gelidium* (J.Agardh) D.P.Cheney et P.W. Gabrielson in Gabrielson and Cheney 1987: 483.

Heterotypic Synonyms: Eucheuma acanthocladum (Harvey) J.Agardh 1876: 600; *Eucheuma echinocarpum* Aresch. 1854: 349; *Meristotheca echinocarpa* (Aresch.) E.J.Faye et Masuda in E.J.Faye et al. 2004: 254; *Meristiella echinocarpa* (Aresch.) D.P.Cheney et P.W.Gabrielson 1987 in Gabrielson and Cheney 1987: 483; *Eucheuma schrammii* (P.Crouan et H.Crouan) J.Agardh 1892: 124; *Meristotheca schrammii* (P.Crouan et H.Crouan) J.H.Price, D.M.John et G.W.Lawson 1986: 90; *Meristiella schrammii* (P.Crouan et H.Crouan) D.P.Cheney et P.W.Gabrielson in Gabrielson and Cheney 1987: 483.

Puerto Rican Records: As *Meristotheca gelidium*: Ballantine et al. 2016b. As *Eucheuma acanthocladum*: Almodóvar 1964a; Navarro and Almodóvar 1974. As *Meristiella gelidium*: Díaz-Piferrer and Caballer de Pérez 1964; Ballantine and Aponte 1997a, 2002a. As *Meristiella echinocarpa*: Ballantine and Aponte 2002a. As E*ucheuma echinocarpum*: Almodóvar and Blomquist 1961; Almodóvar 1964a; Almodóvar and Ballantine 1983; Ballantine et al. 1987. As *Eucheuma gelidium*:

FIGURE 80. *Meristotheca cylindrica*. (A) In situ photograph, algal plain, seaward of Punta Brea, 17 m. Field is approximately 30 cm. (B) DLB8383, herbarium specimen, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 5.0 cm.

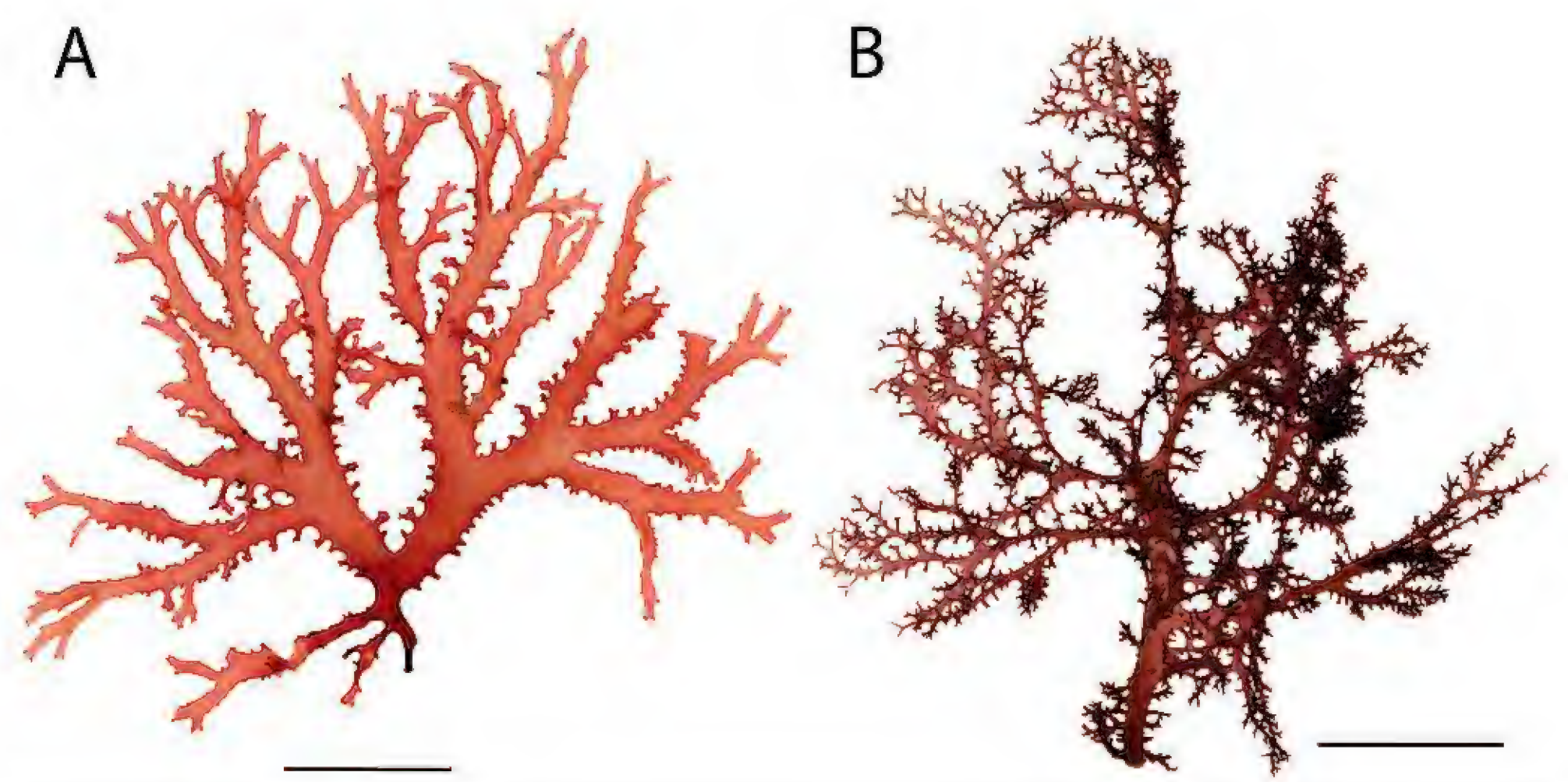

FIGURE 81. *Meristotheca gelidium*. (A) DLB7292, herbarium specimen, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 2.0 cm. (B) DLB6519, herbarium specimen, Guajataca, intertidal rocks. Scale bar = 2.0 cm.

Taylor 1960. As *Eucheuma schrammii*: Almodóvar 1970; Díaz-Piferrer 1970; Almodóvar and Ballantine 1983. As *Meristiella schrammii:* Ballantine and Aponte 2002a.

Western Atlantic Distribution: Caribbean Mexico, Panama, United States (Florida, North Carolina), Barbados, Guadeloupe, Puerto Rico, U.S. Virgin Islands, Brazil.

World Distribution: See Guiry and Guiry 2024.

Type Locality: "In mari Indiae occidentalis."

Thalli are firm, fleshy, or, most commonly, cartilaginous, particularly when mature. Erect axes, 10–30 cm tall, are nearly terete, compressed, or, most commonly, flattened. The principal axes measure 3.0–15 mm broad. Branching is irregularly alternately pinnate, subdichotomous, palmate, or secund. Thallus margins are subentire, with spur branchlets or densely spinulose proliferations, 4.0–36 mm long. Structurally, the axes possess a filamentous medulla of loosely intertwined filaments, 4.0–14 µm diam., surrounded by a 3–9-layered cortex. Inner cortical cells measure 150–300 µm diam., and outermost cortical cells measure 5.0–20 µm diam. Reproductively, the species demonstrates an isomorphic alternation of generations; however, male gametophytes are unknown. Cystocarps, 800–1,000 µm diam., are apiculate but hardly project above the thallus surface. Ovoid tetrasporangia, 10–30 µm diam. and 35–50 µm long, are situated on outer cortical cells. Algae are pale yellow to deep red in color.

Habitat and Comments: *Meristotheca gelidium* has commonly been collected at the Media Luna algal plain. The species has a broad range of differing morphological characters, as might be inferred from the large number of synonymies above. In Puerto Rico, *Meristotheca gelidium* has gone by the epithets *Eucheuma acanthocladum*, *E. echinocarpum*, *E. gelidium*, and *E. schrammi*. Schneider et al. (2020) discussed the somewhat convoluted taxonomic history of *Meristotheca gelidium* and its similarities to *Meristotheca odontoloma* C.W.Schneid., E.S.Peterson et G.W.Saunders from Bermuda. The two are separated on the bases of the former species being fundamentally prostrate, smaller in overall size, and possessing smaller cortical cells and smaller tetrasporangia. [Additional illustrations: as *Eucheuma?* cf. *schrammii*, Norris and Bucher 1982: fig. 101; as *Meristiella gelidium*, Schneider and Searles 1991: figs. 348, 349; Braune and Guiry 2011: fig. 140.1; as *Meristiella schrammii*, Littler and Littler 2000: 99; Littler et al. 2008: 110; as *Meristotheca gelidium*, Littler et al. 2008: 110.]

Solieria J.Agardh

Solieria J.Agardh 1842: 157.

Thalli are erect and irregularly radially branched, with terete or slightly compressed axes. Branches are basally constricted. Axes are multiaxial, with a loosely filamentous medulla surrounded by a pseudoparenchymatous cortex. The cortex is composed of anticlinal files of thin-walled cells. The life history involves an alternation of isomorphic generations. Spermatangia occur in scattered sori. Carpogonial branches are 3–4-celled. Cystocarps are immersed but partially projecting. Zonately divided tetrasporangia occur in sori. One of the 10 recognized *Solieria* species is known from Puerto Rico.

Solieria filiformis (Kütz.) P.W.Gabrielson

FIGURE 82

Solieria filiformis (Kütz.) P.W.Gabrielson 1985: 278, figs. 1b,d, 2.

Basionym: *Euhymenia filiformis* Kütz. 1863: 15.

Heterotypic Synonym: Solieria tenera (J.Agardh) M.J.Wynne et W.R.Taylor 1973: 100.

Misapplied Name: Agardhiella tenera sensu Taylor 1960: 456 [non *Agardhiella tenera* (J.Agardh) F.Schmitz 1897: 371] (=*Agardhiella subulata* (C.Agardh) Kraft et M.J.Wynne)].

Puerto Rican Records: As *Solieria filiformis*: Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002a; Ballantine et al. 2016b. As *Solieria tenera*: Almodóvar and Ballantine 1983. As *Agardhiella tenera* sensu Taylor 1960.

Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina, South Carolina, Georgia, Florida), Antigua, Bahamas, Barbados, Costa Rica, Cuba, Guadeloupe, Hispaniola, Martinique, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Antigua.

Thalli are bushy, reaching ~30 cm in height. The firm, fleshy axes, 0.5–1.9 mm diam., are terete and 1–3 times alternately radially branched. Branches are basally constricted, and thalli are firmly fleshy in texture. The medulla is composed of filaments, 10–20 µm diam., and rhizoids, 2.0–12 µm diam. The medulla is surrounded by a 3–4-layered inner cortex of ovoid cells, 60–160 µm diam., and a middle and outer cortical layer.

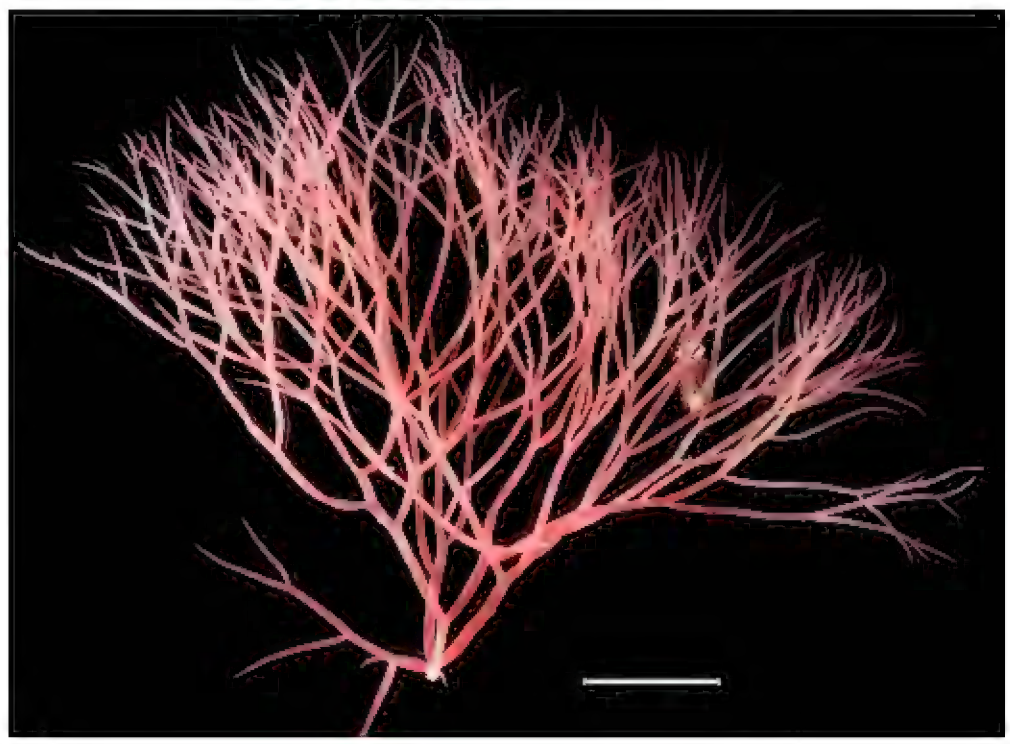

FIGURE 82. *Solieria filiformis*. Live specimen, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 2.0 cm.

Surface cells measure 5.0–15 µm diam. Gametophytes are dioecious. Ovoid to ellipsoid spermatangia, 2.0 µm diam. and 3.0 µm long, are found in surface patches. Globose cystocarps measure 0.5–1.0 mm diam. Ovoid tetrasporangia, 15–35 µm diam. and 30–55 µm long, occur in the outer cortex. Algae are deep rose red to pinkish translucent in color.

Habitat and Comments: *Solieria filiformis*, commonly at the offshore algal plains, has also been collected to 36 m depth in Puerto Rico. [Additional illustrations: Wynne and Taylor 1973: figs. 1–6; Littler et al. 2008: 111.]

Wurdemannia Harv.

Wurdemannia Harv. 1853: 245.

Thalli are tufts or turfs to 5.0 cm in height, developed from entangled rhizomatous bases that are attached by multiple haptera. Erect terete axes are wiry and multiaxial, with several small apical cells. Branching is limited and irregular, alternate, or pinnate. The axes are composed of longitudinally elongate medullary cells that appear pseudoparenchymatous in section. Gametophytic reproduction is uncommon. Zonate tetrasporangia are aggregated in slightly swollen tips of fertile axes. *Wurdemannia* is considered to be a monotypic genus.

Note: Silva et al. (1996) and others have treated *Wurdemannia* as a genus of uncertain taxonomic placement. The status and placement of *Wurdemannia* within the Solieriaceae were resolved molecularly by Saunders et al. (2004).

Wurdemannia miniata (Spreng.) Feldmann et Hamel

FIGURE 83

Wurdemannia miniata (Spreng.) Feldmann et Hamel 1934: 544.

Basionym: *Sphaerococcus miniatus* Spreng. 1827: 340.

Puerto Rican Records: As *Wurdemannia miniata*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002a; Ballantine et al. 2016b.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Bermuda, Bahamas, Belize, Costa Rica, El Salvador, Jamaica, Martinique, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: French Mediterranean.

Thalli occur in tufts or turfs, reaching to 3.0 cm in height. Thalli are entangled and rhizomatous or flagelliform below, attached by multiple haptera. Erect axes, 150–400 µm diam., are sparingly irregularly branched. Branches are attenuated terminally. Medullary cells, to 250 µm diam., are thick-walled. Surface cortical cells measure 6.0–12 µm diam. Ovoid tetrasporangia, 23–26 µm diam. and 48–55 µm long, are scattered over distal parts of slightly enlarged branchlets. Algae are dull red in color.

FIGURE 83. *Wurdemannia miniata*. MDP300, herbarium specimen, Guánica. Scale bar = 1.0 cm.

Habitat and Comments: *Wurdemannia miniata* is typically known as being from shallow water (Taylor 1960), although it is also a member of the deepwater turf community in Puerto Rico, where it has been collected to 63 m depth (Ballantine et al. 2016b). [Additional illustrations: Joly et al. 1965a: pl. 3: figs. 6–8.]

Gracilariales Fredericq et Hommers.[7]

Gracilariaceae Subfam. Gracilarioideae Stizenb.

Gracilarioideae Tribe Gracilariopsideae Gurgel, J.N.Norris et Fredericq

Hydropuntia Montagne Subgen. *Polycavernosa* (C.F.Chang et B.-M.Xia) Gurgel, J.N.Norris et Fredericq

Crassiphycus Guiry, J.N.Norris, Fredericq et Gurgel in Guiry et al. 2018: 1.

Synonym: Crassa Gurgel, J.N.Norris et Fredericq in Gurgel et al. 2018: 10 nom inval.

[7] Contributed by Carlos Frederico D. Gurgel, Universidade Federal do Rio de Janeiro, Instituto de Biodiversidade e Sustentabilidade - NUPEM, Av. São José Barreto 764, São José do Barreto, Macaé, RJ 27965-045, Brazil; Suzanne Fredericq, University of Louisiana at Lafayette, Department of Biology, Lafayette, Louisiana, USA.; James N. Norris; David L. Ballantine; and H. Ruiz.

Thalli are erect and may be terete, compressed, or flattened. Female gametophytes have a unique spherical gonimoblast mass (placenta) with a sharp transition between the gonimoblasts and upper short, usually dichotomously branched chains of carposporangia. Cystocarps have a distinctive, wel-defined flat floor. Gametophytic fusion cells are dendritic. Spermatangia form deep conceptacles that are often confluent, giving rise to multiple cavities in the medulla when seen in transverse section. (Guiry et al. 2018; Gurgel et al. 2018).

Three of the 11 known species of *Crassiphycus* occur in Puerto Rico. The species of *Crassiphycus* are included in the key below. Different interpretations of the genetic analyses of species led Lyra et al. (2016) to consider *Crassiphycus* synonymous with *Gracilaria*. Herein we follow the phylogenetic analysis and conclusions of Gurgel et al. (2018, 2021).

KEY TO THE *CRASSIPHYCUS*, *GRACILARIA*, AND *GRACILARIOPSIS* SPECIES OF PUERTO RICO

1. Main axes flattened, at least distally 2
   Main axes cylindrical or compressed 8
2. Complanate branching is marginal and opposite to pinnate . . . . . *Gracilaria domingensis*
   Branching not opposite to pinnate 3
3. Sparingly branched in 1 or a few degrees 4
   Branched in several degrees 7
4. Blades crisp with ruffled margins . . . . . *Gracilaria cuneata*
   Blades neither crisp nor with ruffed margins 5
5. Blades to 1.4 mm thick. . . . . *Gracilaria isabellana*
   Blades less than 1.0 mm thick 6
6. Blades 200–350 µm thick, branches constricted at their point of insertion . . . . . *Gracilaria cearensis*
   Blades to 100 µm thick; branches not constricted at their point of insertion . . . . . *Gracilaria hayi*
7. Thalli 7–10 cm tall; apices obtuse . . . . . *Gracilaria mammillaris*
   Thalli not as above. . . . . *Gracilaria tikvahiae*
8. Thalli compressed, sometimes terete distally. 9
   Thalli terete 11
9. Thalli compressed beneath forks, distally terete; branching primarily dichotomous, upper divisions may be secund . . . . . *Gracilaria bursa-pastoris*
   Branching at least partially pinnate 10
10. Branching irregular, pinnate, or alternate below, may be cervicorn above. . . . . *Gracilaria ferox*
    Branching pinnately branched, becoming complanate . . . . . *Gracilaria cervicornis*
11. Thalli decumbent, axes to 5.0 mm thick. . . . . *Crassiphycus crassissimus*
    Thalli erect, axes less than 5.0 mm thick 12
12. Branches constricted at their bases 13
    Branches not constricted at their bases 15
13. Main axes sparingly branched, 2.0–4.0 mm diam. . . . . *Gracilaria cylindrica*
    Main axes abundantly branched, ~0.5–2.0 mm diam. 14
14. Medullary cells thick walled, to 930 µm diam.; intracellular spaces absent . . . . . *Gracilaria blodgettii*
    Medullary cells thin-walled, to 650 µm diam.; intracellular spaces present. . . . . *Gracilaria hummii*
15. Thalli narrower, 4.0 mm or less in diam. 16
    Thalli coarse, typically more than 4.0 mm diam. 17
16. Spermatangia occur in superficial sori . . . . . *Gracilariopsis carolinensis*
    Spermatangia occur in pits . . . . . *Crassiphycus caudatus*
17. Thalli sparsely branched, 3.0–6.0 mm diam.; horny when dried. . . . . *Crassiphycus corneus*
    Thalli abundantly branched, 1.5–4.0 mm diam. . . . . *Gracilaria damicornis*

Crassiphycus caudatus (J.Agardh) Gurgel, J.N.Norris et Fredericq

FIGURE 84

Crassiphycus caudatus (J.Agardh) Gurgel, J.N.Norris et Fredericq in Guiry et al. 2018: 1.

Basionym: Gracilaria caudata J.Agardh 1852: 598.

Homotypic Synonyms: Hydropuntia caudata (J.Agardh) Gurgel et Fredericq 2004: 155; *Crassa caudata* (J.Agardh) Gurgel, J.N.Norris et Fredericq in Gurgel et al. 2018: 10, nom. inval.

Puerto Rican Records: As *Gracilaria caudata*: Almodóvar and Blomquist 1961; Almodóvar 1964a; Díaz-Piferrer and Caballer de Pérez 1964; Ortiz Sotomayor 1976; Almodóvar and Ballantine 1983; Plastino and Oliveira 1997; Ballantine and Aponte 2002a.

FIGURE 84. *Crassiphycus caudatus*. DLB8389, herbarium specimen, Ballena Bay, Guánica, 1.0 m. Scale bar = 2.0 cm.

Western Atlantic Distribution: Caribbean Mexico, Panama, United States (Florida), Bermuda, Bahamas, Barbados, Belize, Guadeloupe, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, St. Barthélemy, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Argentina, Brazil, Colombia, Venezuela.

Syntype Localities: "In mari Indiae occidentalis ad Insulam St. Crucis in sunu Mexicano" (Agardh 1852).

Lectotype Locality: St. Croix, U.S. Virgin Islands (Gurgel et al. 2018).

Thalli are cartilaginous, reaching up to 14–22(–60) cm in height. Terete axes, 0.5–2.0(–3.0) mm diam., possess acute apices. Branching is radially alternate or irregular. The branches are not constricted at their points of insertion. Structurally, thalli possess a 7–8-layered pseudoparenchymatous medulla, consisting of irregular to elongate cells, 30–90 × 50–160 µm diam. The cortex consists of abruptly smaller cells. A 2-layered subcortex possesses elongate cells, 12–18 µm diam. The peripheral cortex possesses a single layer of spherical cells, 4–8 µm diameter. Spermatangia occur in pits in the cortex of younger thallus portions. Hemispherical cystocarps measure to 1.0 mm diam. Spherical tetrasporangia measure 20–45 µm diam. Algae are reddish purple or green in color.

Habitat and Comments: *Crassiphycus caudatus* has been collected in algal plains growing on shell fragments and coral rubble. [Additional illustrations: as *Gracilaria caudata*, Plastino and Oliveira 1997: figs. 1–12; Littler and Littler 2000: 113; Lyra et al. 2021: fig. 5.]

Crassiphycus corneus (J.Agardh) Gurgel, J.N.Norris et Fredericq

FIGURE 85

Crassiphycus corneus (J.Agardh) Gurgel, J.N.Norris et Fredericq in Guiry et al. 2018: 1.

Basionym: *Gracilaria cornea* J.Agardh 1852: 598.

Homotypic Synonyms: *Hydropuntia cornea* (J.Agardh) M.J.Wynne 1989: 476; *Crassa cornea* Gurgel, J.N.Norris et Fredericq in Gurgel et al. 2018: 10; *Gracilaria debilis* sensu Taylor 1960 [non *Gracilaria debilis* (Forssk.) Børgesen 1932: 7].

Misapplied Name: *Gracilaria debilis* sensu Taylor 1960 [non *G. debilis* (Forssk.) Børgesen 1932: 7.

Puerto Rican Records: As *Gracilaria debilis*: Taylor 1960; Navarro and Almodóvar 1974; Ortiz Sotomayor 1976. As *Gracilaria cornea* (Turner) J.Agardh: Hauck 1888; Ballantine and Aponte 1997a. As *Hydropuntia cornea*: Ballantine and Aponte 2002a.

Western Atlantic Distribution: Caribbean Mexico, Bermuda, Bahamas, Belize, Grenadines, Guadeloupe, Hispaniola, Jamaica, Puerto Rico, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Pernambuco(?), Brazil (Bird et al. 1986; Gurgel et al. 2018).

Bushy thalli are coarse in texture and up to 30 cm in height. Subterete axes, 3.0–6.0 mm wide, are irregularly alternately branched and become cervicorn distally. Secund branchlets are short and frequently arcuate. Medullary cells, 200–320 µm diam., are thick-walled and gradually grade to a 3–7-layered cortex. Subcortical cells are 35–70 µm diam., and outer cortical cells are smaller, rounded or oval, 5.4–7.5 µm in diameter. Tetrasporangia and spermatangia have not been found in Puerto Rican specimens. Hemispherical, apiculate cystocarps, 0.5–1.25 mm diam., are formed marginally in the more slender branches. Tetrasporangia measure 6.0–8.0 µm diam. and 15–20 µm long. Algae are reddish brown to greenish brown in color.

Habitat and Comments: *Crassiphycus corneus*, the generitype (Guiry et al. 2018; Gurgel et al. 2018: 10), was originally reported in the Caribbean as "*Gracilaria debilis*" from among its known multiple morphologies. Later, Bird et al. (1986) noted the holotype species, *Fucus debilis* Forssk. (1775: Type Locality: Yemen), was reproductively distinct from those western Atlantic "*G. debilis*" and corrected its name to *G. cornea* J.Agardh (=*Hydropuntia cornea* (J.Agardh) M.J.Wynne). Other species that were sometimes incorrectly referred to "*G. debilis*" include *C. usneoides* (C.Agardh) Gurgel, J.N.Norris et Fredericq and *C. crassissimus*.

In Puerto Rico, *Crassiphycus corneus* is known from shallow inshore habitats to offshore algal plains. Specimens are straw colored to pink in color when alive; specimens dry to a

FIGURE 85. *Crassiphycus corneus*. (Left) Live specimen, algal plain, 1.5 km seaward Media Luna Reef, 17 m, La Parguera. Scale bar = 2.0 cm. (Right) DLB2331, herbarium specimen, Guayacan Island, La Parguera, adrift. Scale bar = 5.0 cm.

dull grayish brown. [Additional illustration: as *Gracilaria debilis*, Taylor 1960: pl. 57: fig. 3.]

Crassiphycus crassissimus (P.Crouan et H.Crouan) Gurgel, J.N.Norris et Fredericq

FIGURE 86

Crassiphycus crassissimus (P.Crouan et H.Crouan) Gurgel, J.N.Norris et Fredericq in Guiry et al. 2018: 1.

Basionym: *Plocaria crassissima* P.Crouan et H.Crouan in Schramm and Mazé 1865: 20.

Homotypic Synonyms: *Gracilaria crassissima* (P.Crouan et H.Crouan) P.Crouan et H.Crouan in Schramm and Mazé 1866: 46; *Polycavernosa crassissima* (P.Crouan et H.Crouan) Fredericq et J.N.Norris 1985: 152, nom. inval.; *Hydropuntia crassissima* (P.Crouan et H.Crouan) M.J.Wynne 1989: 477; *Crassa crassissima* (P.Crouan et H.Crouan) Gurgel, J.N.Norris et Fredericq in Gurgel et al. 2018: 10, nom. inval.

Puerto Rican Records: As *Gracilaria crassissima*: Taylor 1960; Almodóvar 1964a, 1964b, 1965; Díaz-Piferrer and Caballer de Pérez 1964; Ortiz Sotomayor 1976; Ballantine and Aponte 1997a. As *Polycavernosa crassissima*: Almodóvar and Ballantine 1983. As *Hydropuntia crassissima*: Ballantine and Aponte 2002a.

Western Atlantic Distribution: Belize, Panama, United States (Florida), Bermuda, Bahamas, Barbados, Guadeloupe, Hispaniola, Martinique, Puerto Rico, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Reefs at Moule Port entrance, Moule, Guadeloupe, French West Indies.

Thalli are coarse, cartilaginous, and spreading to 10–30 cm in extent, attaching at numerous points. Axes are mostly flattened, to 5.0 mm thick and 2.0 cm broad, and grow in a decumbent and spreading manner. Branching is closely irregularly alternate, and

FIGURE 86. *Crassiphycus crassissimus*. MDP2991, herbarium specimen, Cabo Rojo. Scale bar = 2.0 cm.

the branchlets may become entangled. Structurally, axes possess a medulla of large thick-walled cells, ~380(–460) µm diam. The outer cortex consists of oval, radially positioned cells, 4.0–10 µm diam. and 8.0–15 µm long. Tetrasporangia measure to 20 µm diam. Algae are dull, pale reddish brown in color, sometimes mottled.

Habitat and Comments: In Puerto Rico, *Crassiphycus crassissimus* (as *Gracilaria crassissima*) is found on hard substrata in a variety of habitat types. Normally encountered in shallow water, the species has been collected to 15 m depth. Thalli may shrink substantially on drying. [Additional illustrations: as *Gracilaria crassissima*, Taylor 1960: pl. 55: fig. 4; Fredericq and Norris 1985: figs. 4, 18, 20, 21, 23, 72; Littler and Littler 2000: 121.]

Gracilarioideae Tribe Gracilarieae Willk.

Gracilaria Grev.

Gracilaria Grev. 1830: 121.

Erect or partially decumbent fleshy or cartilaginous thalli arise from a discoid holdfast. Axes are terete, compressed, or flattened, and branching is dichotomous, pinnate, or irregular. Thalli possess a medulla of large colorless cells that grade to smaller-diameter cells outwardly and a 2–6-layered cortex. Gametophytes are dioecious. Carpogonial branches are 2 cells long, and auxiliary cells are absent. Gonimoblast filaments are issued directly from fusion cells. Cystocarps protrude from the female gametophytes. Spermatangia occur in shallow cortical conceptacles, with very few exceptions. Cruciately divided tetrasporangia occur among unmodified cortical cells or in sori. There are 14 species, including 2 of uncertain generic placement, of *Gracilaria* in Puerto Rico; 171 are recognized worldwide.

Comments: Substantial vegetative polymorphism among *Gracilaria* species has made morphological-based systematics difficult. According to Guiry and Guiry (2024), all terete *Gracilaria* species from the NE Atlantic and elsewhere require individual examination to determine whether they belong to *Gracilaria*, *Gracilariopsis*, *Hydropuntia*, or *Crassiphycus*. Spermatangia in *Gracilaria* sensu stricto are characterized by shallow cortical conceptacles with the exception, so far, of the phylogenetically closely related *Gracilaria domingensis* and *Gracilaria baiana* Lyra, Gurgel, M.C.Oliveira et J.M.C.Nunes (2016), in which cortical conceptacles are embedded deeper into the thallus surrounded by secondary cortical cell development.

Gracilaria subgen. *Gracilaria*

Gracilaria blodgettii Harv.

FIGURE 87

Gracilaria blodgettii Harv. 1853: 111.

Puerto Rican Records: Ortiz Sotomayor 1976; Ballantine et al. 1987; Fredericq and Norris 1992; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina, South Carolina, Georgia, Florida), Cuba, Hispaniola, Jamaica, Martinique, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Key West, Florida, USA.

Thalli are erect and cartilaginous, reaching to ~20 cm in height. Branching is radially alternate to 2–4 orders. Principal axes measure to 2.0 mm diam., and branchlets measure from 0.5 to 1.0 mm diam. Axes are cylindrical, and branches are strongly constricted at their point of insertion. Branch tips are acute. Structurally, axes possess a medulla of large thick-walled and colorless cells, to 930 µm diam., surrounded by a much smaller 1–2-layered inner cortex and a single-layered outer cortex. Peripheral cortical cells measure 12–20 µm diam. Spermatangia occur in shallow sori in the outer cortex. Cystocarps, to 1.0 mm diam., substantially project from branches. Ovoid to spherical carposporangia are to 40 µm long. Spherical tetrasporangia measure 20–50 µm diam. Algae are light pink in color.

Habitat and Comments: *Gracilaria blodgettii* commonly occurs at mid-depth habitats, including the offshore algal plains on the Puerto Rican southern coast. [Additional illustrations: Børgesen 1909: fig. 11; Schneider and Searles 1991: figs. 370, 371.]

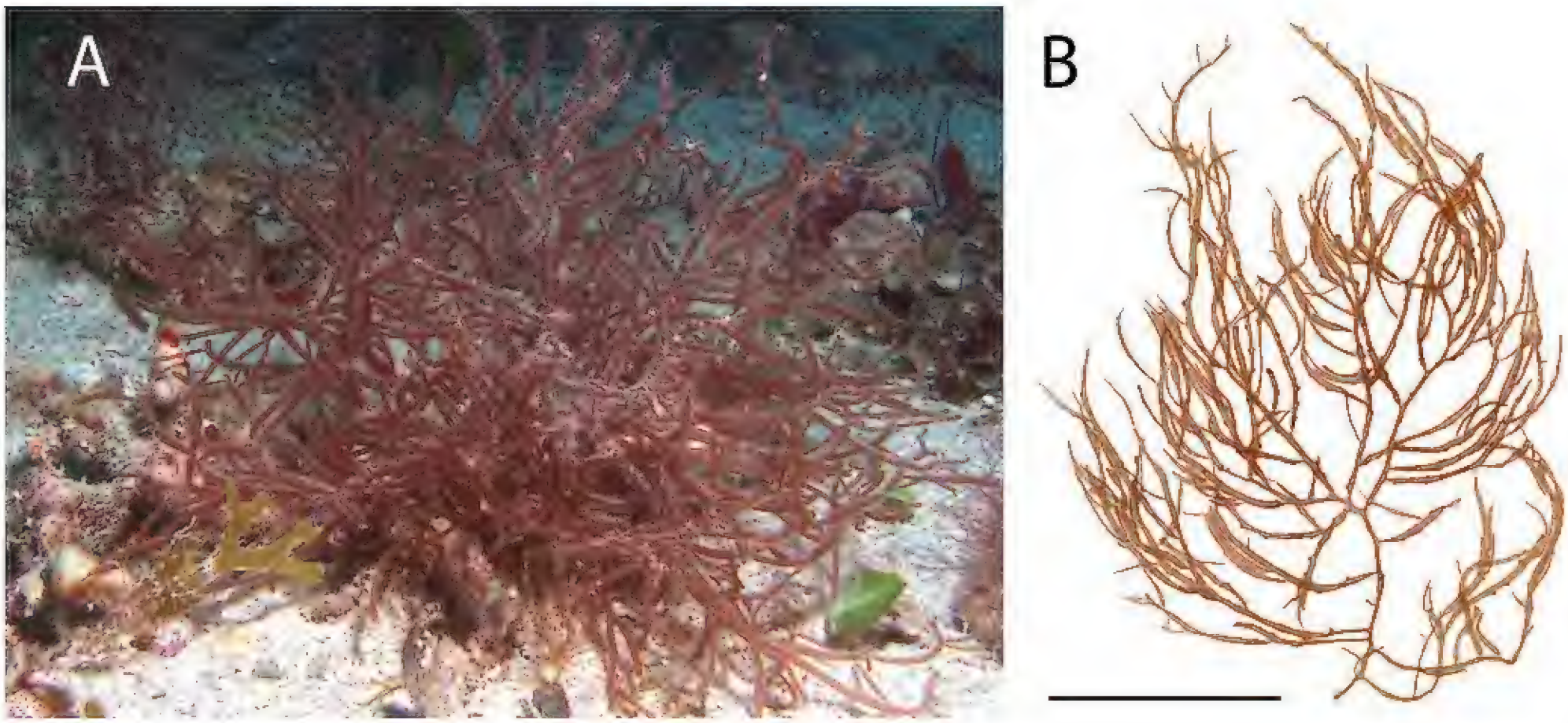

FIGURE 87. *Gracilaria blodgettii*. (A) In situ photograph, 1.5 km seaward Media Luna Reef, 17 m. Field is approximately 25 cm. (B) DLBsn, herbarium specimen, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 5.0 cm.

Gracilaria bursa-pastoris (S.G.Gmel.) P.C.Silva

FIGURE 88

Gracilaria bursa-pastoris (S.G.Gmel.) P.C.Silva 1952: 265.

Basionym: *Fucus bursa-pastoris* S.G.Gmel. 1768: 121, pl. VIII: fig. 3.

Heterotypic Synonym: Gracilaria compressa (C.Agardh) Grev. 1830: liv, 125.

Puerto Rican Records: As *Gracilaria bursa-pastoris*: Ortiz Sotomayor 1976; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002a. As *Gracilaria compressa*: Díaz-Piferrer 1963; Navarro and Almodóvar 1974; Ballantine 1979; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Cuba, Guadeloupe, Jamaica, Martinique, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Mediterranean Sea (Silva et al. 1996).

Lectotype: Original illustration of Gmelin (1768: pl. VIII: fig. 3) selected by Dixon and Irvine (1977).

Erect fleshy thalli reach 15–25 cm in height. Branching is irregularly dichotomous proximally and radially alternate to secund distally. Axes are terete; however, they are moderately compressed at mid-thallus level and below the divisions, 1.0–4.0 mm wide. Branches are attenuated at their tips. Medullary cells, to 300 µm diam., are thin walled and grade into a 1–3-celled cortex. Inner cortical cells measure 9.0–25 µm diam., and outer cortical cells are 8.0–9.0 µm diam. Protruding ovate to hemispherical cystocarps are scattered. Algae are reddish brown to rose purple in color.

Habitat and Comments: *Gracilaria bursa-pastoris* is commonly collected at the Media Luna algal plain at a depth of 17 m. Spermatangia were not observed in Puerto Rican specimens, and status of the species in Puerto Rico requires further study.

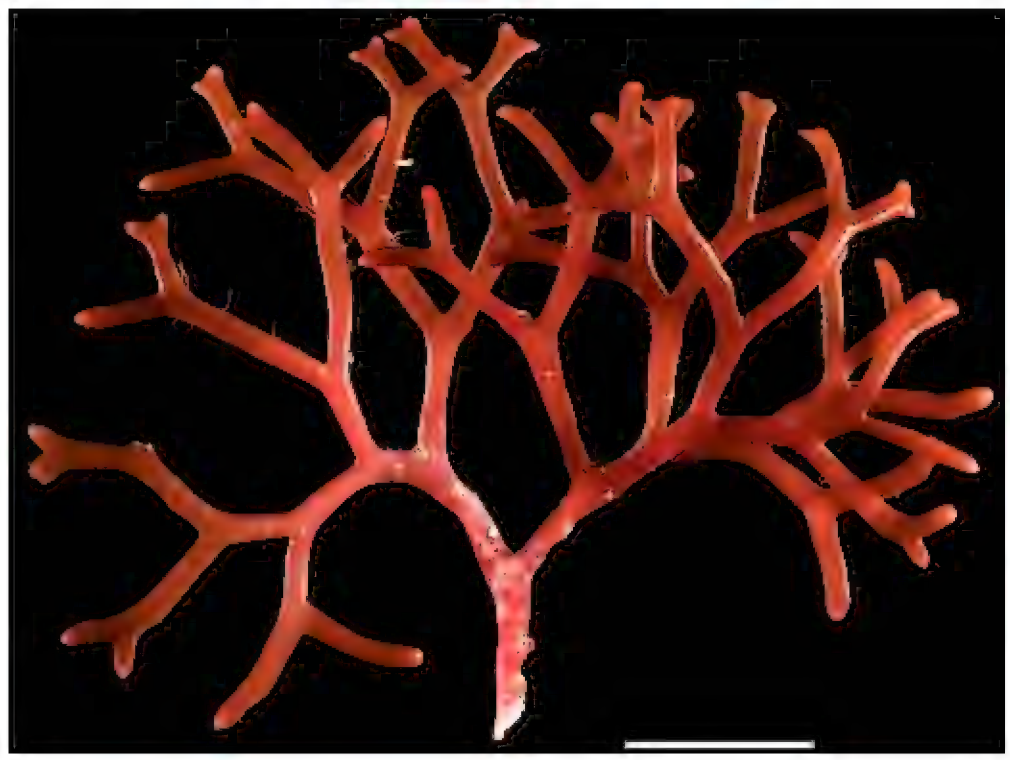

FIGURE 88. *Gracilaria bursa-pastoris*. DLB7299, live specimen, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 2.0 cm.

Gracilaria cearensis (A.B.Joly et Pinheiro) A.B.Joly et Pinheiro

FIGURE 89

Gracilaria cearensis (A.B.Joly et Pinheiro) A.B.Joly et Pinheiro in Pinheiro and Joly 1966: 131.

Basionym: *Tylotus cearensis* A.B.Joly et Pinheiro in Joly et al. 1965b: 81, pl. V.

Heterotypic Synonym: Gracilaria smithsoniensis Gurgel, Fredericq et J.N.Norris 2004a: 187, fig. 10A–G.

Misapplied Names: Gracilaria cuneata Aresch. 1854: 351; *Gracilaria curtissiae* J.Agardh 1885: 61.

Puerto Rican Records: The species is newly reported from Puerto Rico herein. DLBsn (US Alg. Coll. 221500), 3.vi.1975, at Ballena Bay, Guánica, 1.0–2.0 m depth (as *G. cuneata*); M.Diaz Piferrer1132 (US Alg. Coll. 94633), 8.ix1961, subtidally at Playa Tamarindo, Guánica (as *G. curtissiae* J.Agardh).

West Atlantic Distribution: Panama, Puerto Rico, Brazil.

Type Locality: Fortaleza, Ceará, Brazil.

Thalli are 3.0–25 cm high above a basal stipe, to 5.0 cm long. The flattened, strap-like branches measure 2.0–12 mm wide and 200–350 µm thick. Branches possess entire margins, sometimes with proliferations and rounded apices. Algae branch mostly dichotomously and not infrequently trichotomously. Branches are constricted at their origins, and branching dichotomies tend to be narrow. The medulla is composed of 3–6 layers of thick-walled cells, measuring 17–50 × 120–180 µm. Surrounding the medulla are 1–3 layers of cortical cells, measuring 5.0–8.0 × 1.5–10 µm. The thickened thallus base possesses an anticlinal series of up to 7 cortical cells. Cruciately divided tetrasporangia measure 20– 30 µm. Spermatangia form irregular extensive sori over the thallus surface in shallow conceptacles of shallow conceptacles (textorii type) over the surface. Hemispherical cystocarps measure 1.0–2.0 mm diam. Algae are frequently bright red in color.

Habitat and Comments: In Puerto Rico, *Gracilaria cearensis* occurs on algal-dominated hard benthic substrata in shallow subtidal environments. Puerto Rican specimens agree in all respects with previous published accounts and share the otherwise unusual character of having files of cortical cells oriented at right angles to the plane of the blade in older portions (see Soares et al. 2015: fig. 2A). [Additional illustrations: Soares et al. 2015: figs. 1A–G, 2A–L.]

Gracilaria cervicornis (Turner) J.Agardh

FIGURE 90

Gracilaria cervicornis (Turner) J.Agardh 1852: 604.

Basionym: *Fucus cervicornis* Turner 1808: 131–132, pl. 121.

Heterotypic Synonym: *Gracilaria ferox* J.Agardh 1852: 592.

Puerto Rican Records: As *Gracilaria cervicornis*: Hauck 1888; Taylor 1960; Díaz-Piferrer and Caballer de Pérez 1964; Navarro and Almodóvar 1974; Ortiz Sotomayor 1976; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, Panama, United States (Florida), Bermuda, Bahamas, Barbados, Belize, Guadeloupe, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, St. Barthélemy, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Argentina, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Lectotype Locality: Jamacia fide Lyra et al. 2016.

Erect thalli reach 8.0–40 cm in height. Axes are terete to compressed, 2.0–5.0 mm broad and pinnately branched, becoming

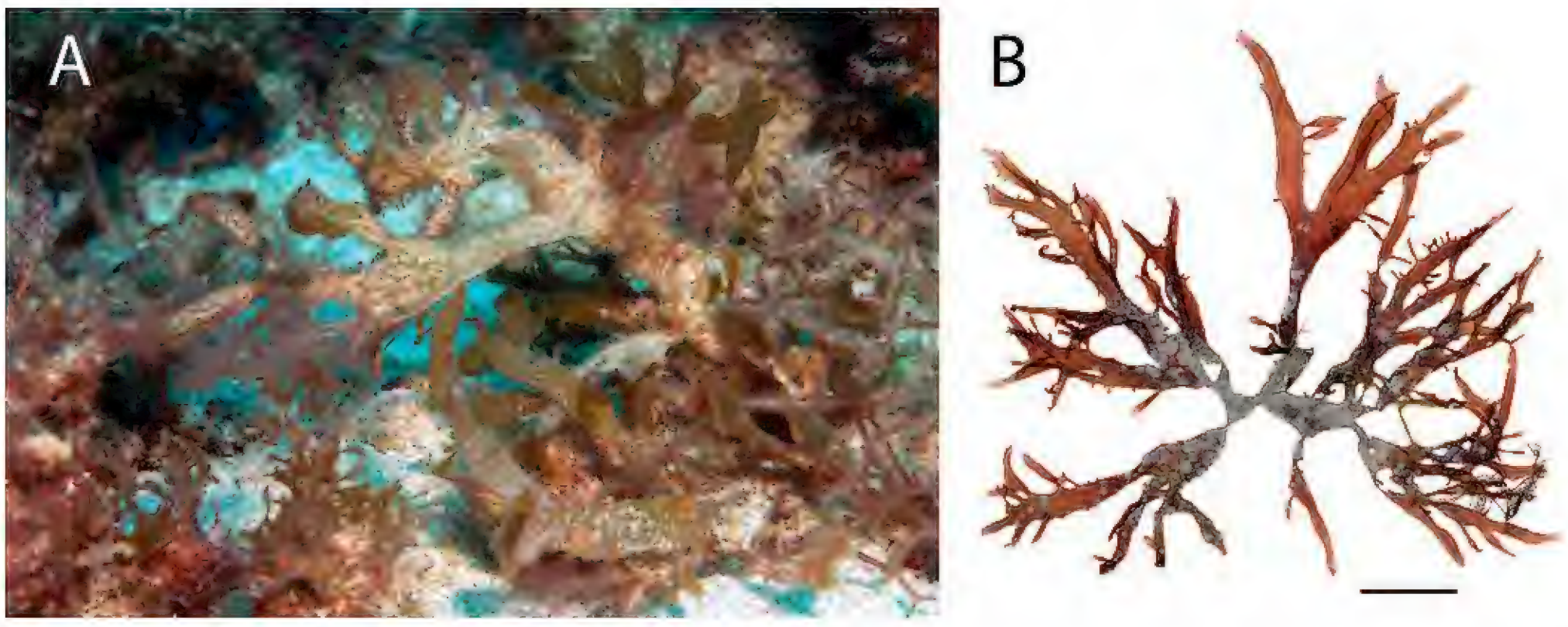

FIGURE 89. *Gracilaria cearensis*. (A) In situ photograph, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Field is approximately 20 cm. (B) DLB2127, herbarium specimen, Ballena Bay, Guánica, 1.0 m. Scale bar = 2.0 cm.

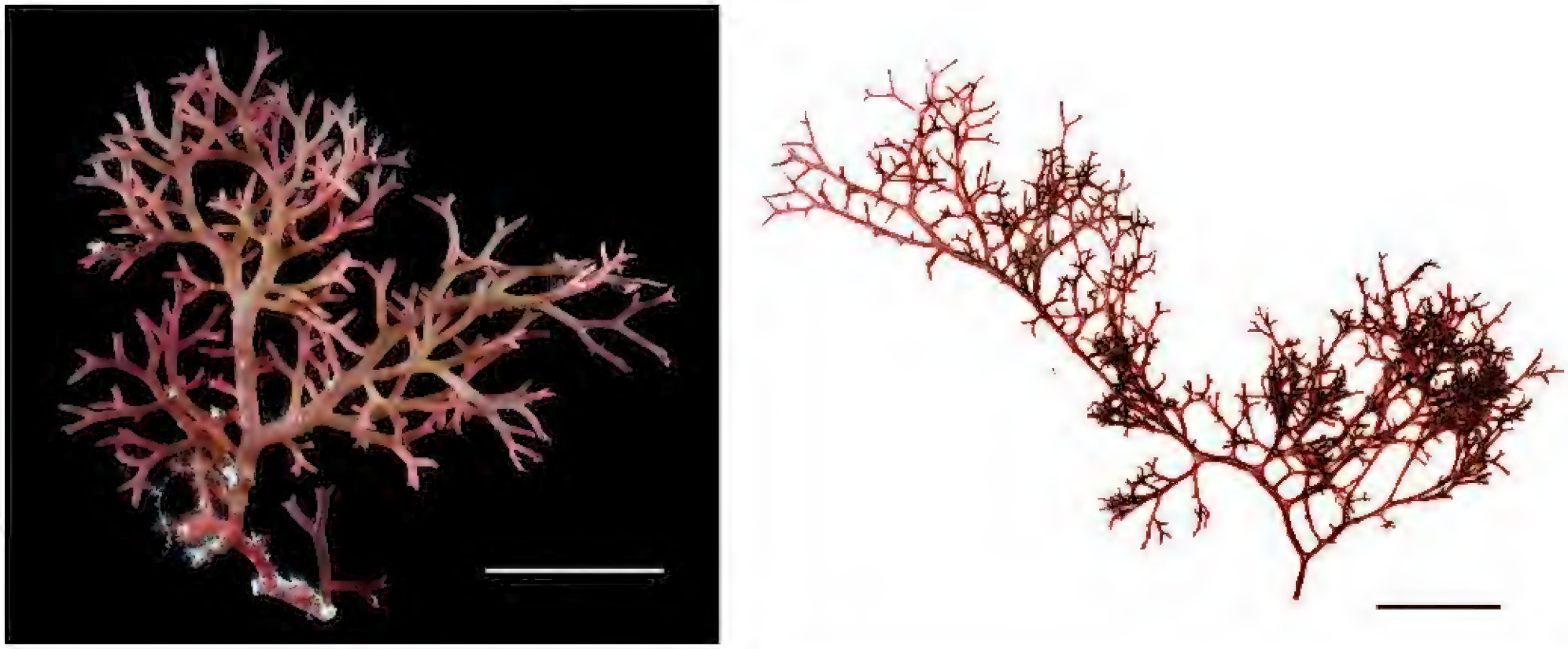

FIGURE 90. *Gracilaria cervicornis*. (Left) Live specimen. Scale bar = 2.0 cm. (Right) DLB7300, herbarium specimen, algal plain, 1.5 km seaward Media Luna Reef, 17 m. Scale bar = 2.0 cm.

cervicorn distally. The axes possess short toothlike projections marginally. Irregularly spherical medullary cells, measuring 175–350 µm diam., occur in 4–6 layers. There is a gradual transition in cell size toward the periphery. Inner cells of the 3–7-layered cortex measure 20–30 µm diam., and the outer cortical cells measure 6.0–10 µm diam. Spermatangia occur in small cavities. Hemispherical, apiculate cystocarps, 0.5–1.25 mm diam., are formed marginally in the more slender branches. Tetrasporangia measure 6.0–8.0 µm diam. and 15–20 µm long. Algae are reddish brown to greenish brown in color.

Habitat and Comments: *Gracilaria cervicornis* typically grows in shallow-water habitats, such as at Ballena Bay, Guánica, and at depths to 20 m. *Gracilaria ferox* and *G. cervicornis* have been treated by some authors as being synonymous; however, they are treated as separate species by Wynne (2017, 2022). [Additional illustrations: Cordeiro-Marino 1978: figs. 154–157; Littler and Littler 2008: 112.]

Gracilaria cuneata Aresch.

FIGURE 91

Gracilaria cuneata Aresch. 1854: 351.

Puerto Rican Records: Ortiz Sotomayor 1976; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Costa Rica, Caribbean Mexico, Panama, United States (Florida), Barbados, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Pernambuco, Brazil.

Lectotype: Selected by Taylor 1969: 174, fig. 25.

FIGURE 91. *Gracilaria cuneata*. DLBsn, herbarium specimen, algal plain offshore from Punta Brea, 17 m. Scale bar = 2.0 cm.

Thalli reach 12–18 cm in height, consisting of a membranous blade above a short subterete stipe, to 1.0 cm long. The blade, 200–300 µm thick, is cuneate at its base and expands above into a blade that is divided into lobes, 5.0–12 mm broad. The medulla consists of 4–5 layers of round cells, 100–180 µm diam., that gradually transition to a 1–2-layered cortex of anticlinally elongated cells. Spermatangia occur in shallow conceptacles in the cortex. Hemispherical cystocarps are scattered. Algae are rosy purple in color.

Habitat and Comments: *Gracilaria cuneata* has been collected in Puerto Rico from 3.0–35 m depths; most collections have been from Ballena Bay, Guánica. Our herbarium studies revealed the name "*Gracilaria cuneata*" has been misapplied to many of the flat-bladed Puerto Rican specimens of *Gracilaria*. [Additional illustrations: Taylor 1969: fig. 25.]

Gracilaria cylindrica Børgesen

FIGURE 92

Gracilaria cylindrica Børgesen 1920: 375, figs. 354, 355.

Puerto Rican Records: Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar 1965; Almodóvar and Blomquist 1965; Ortiz Sotomayor 1976; Almodóvar and Ballantine 1983; Fredericq and Norris 1992.

FIGURE 92. *Gracilaria cylindrica*. DLBsn, herbarium specimen, algal plain, seaward Margarita Reef, 24 m. Scale bar = 2.0 cm.

Western Atlantic Distribution: United States (North Carolina, Florida), Cuba, Guadeloupe, Jamaica, Puerto Rico, U.S. Virgin Islands, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Syntype Localities: North of American Hill, St. John, and between St. John and St. Thomas, U.S. Virgin Islands.

Thalli reach to 40 cm in height. Terete axes, 2.0–4.0 mm diam., are sparingly irregularly or radially alternately branched. The frequently arcuate branches are sharply constricted at their bases and have obtuse tips. The medulla consists of thin-walled cells, 200–525 µm diam. Surrounding the medulla is a 1–2-layered subcortex and 2 layers of cortical cells, 5.0–7.5 µm diam. Cystocarps, to 2.0 mm diam., are scattered and somewhat projecting. Ovoid to spherical carposporangia measure to 40 µm diam. Spermatangia were not found in Puerto Rican specimens. Tetrasporangia, 20–40 µm diam. and 40–60 µm long, are scattered and immersed in the cortex. Algae are rose red in color.

Habitat and Comments: In Puerto Rico, *Gracilaria cylindrica* is known from depths of 18–36 m. Although Fredericq and Norris (1992) proposed *G. cylindrica* and *G. blodgettii* to be synonymous, others have kept them as separate species (Littler and Littler, 2000; Dawes and Mathieson, 2008; Guiry and Guiry 2024). [Additional illustrations: Schneider and Searles 1991: fig. 373; Fredericq and Norris 1992: figs. 4–6, 9, 10; Littler and Littler 2000: 115.]

Gracilaria damicornis J.Agardh

FIGURE 93

Gracilaria damicornis J.Agardh 1852: 597 (as '*damaecornis*').

Puerto Rican Records: As *Gracilaria damaecornis*: Taylor 1960, pro parte; Díaz-Piferrer 1963; Almodóvar 1964a; Ortiz Sotomayor 1976; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

FIGURE 93. *Gracilaria damicornis*. DLB7096, herbarium specimen, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 2.0 cm.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Bermuda, Bahamas, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Barthélemy, St. Lucia, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: "Ad littus Americae borealis in oceano atlantico (Rafn.!)." North American shores of Atlantic Ocean, C. S. Rafinesque (Guiry and Guiry 2024).

Thalli are bushy, reaching to 7.0–15 cm in height, and are cartilaginous in texture. The axes, 1.5–4.0 mm diam., are terete to slightly flattened. Branching is irregularly dichotomous proximally and becomes subsecund distally. Ultimate branches are short. The medulla consists of thin-walled cells, to 200 µm diam. Surface cells of the 2–3-layered cortex measure 8.0–20 µm diam. Tetrasporangia are immersed in the cortex. Cystocarps are hemispherical and protruding. Tetrasporangia are scattered within the cortex. Algae are pale red in color.

Habitat and Comments: *Gracilaria damicornis* is typically an alga of shallow-water habitats. [Additional illustrations: Littler and Littler 2000: 115; Littler et al. 2008: 113; Braune and Guiry 2011: fig. 120.4.]

Gracilaria domingensis (Kütz.) Sond. ex Dickie

FIGURE 94
Gracilaria domingensis (Kütz.) Sond. ex Dickie 1874: 149, pl. 11.
Basionym: *Sphaerococcus domingensis* Kütz. 1869: 8, pl. 22a,b.
Puerto Rican Records: As *Gracilaria domingensis*: Díaz-Piferrer 1963; Almodóvar 1964a, 1965; Díaz-Piferrer and Caballer de Pérez 1964; Navarro and Almodóvar 1974; Ortiz Sotomayor 1976; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002a.
Western Atlantic Distribution: North America, Costa Rica, Cuba, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Panama, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Santo Domingo (Dominican Republic).

Thalli are leathery to cartilaginous in texture, reaching to 35 cm in height. Axes, 4.0–12 mm broad and to 350 µm thick, are strap-shaped to flattened. Branching, to 2 orders, is irregular; however, branching from the margins is pinnate, and the pinnate divisions may redivide. Thin-walled medullary cells, to 600 µm, gradually grade (sharp transition according to Lyra et al. 2016) into the 2–4-layered cortex. Inner cortical cells measure 20–50 µm diam., and the peripheral cortical cells measure 6.0–10 µm diam. Protruding hemispherical cystocarps mainly occur in the lesser branchlets and possess a slight constriction at their bases. Spherical tetrasporangia measure to 45 µm diam. Tetrasporangia, to 20 µm diam. and 35 µm long, are immersed in the cortex. Algae are pale yellow to pink and red in color.

Habitat and Comments: *Gracilaria domingensis* has been collected in Puerto Rico from quite shallow water to depths of 30 m; it is commonly encountered at Ballena Bay, Guánica. Lyra et al. (2016) reported that multiple cryptic species are included in what has been called *G. domingensis*. [Additional illustrations: Taylor 1960: pl. 57: figs. 1, 2; Cordeiro-Marino 1978: figs. 158–161; Lyra et al. 2016: figs. 7, 8; Lyra et al. 2021: fig. 10.]

FIGURE 94. *Gracilaria domingensis*. DLBsn, herbarium specimen, Ballena Bay, Guánica, 1.0 m. Scale bar = 5.0 cm.

Gracilaria ferox J.Agardh

FIGURE 95
Gracilaria ferox J.Agardh 1852: 592.
Puerto Rican Records: Taylor 1960; Almodóvar 1962, 1964a; Almodóvar and Blomquist 1961; Díaz-Piferrer and Caballer de Pérez 1964; Navarro and Almodóvar 1974; Ortiz Sotomayor 1976; Almodóvar and Ballantine 1983.
Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Bermuda, Barbados, Hispaniola, Martinique, Panama, Puerto Rico, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Venezuela.

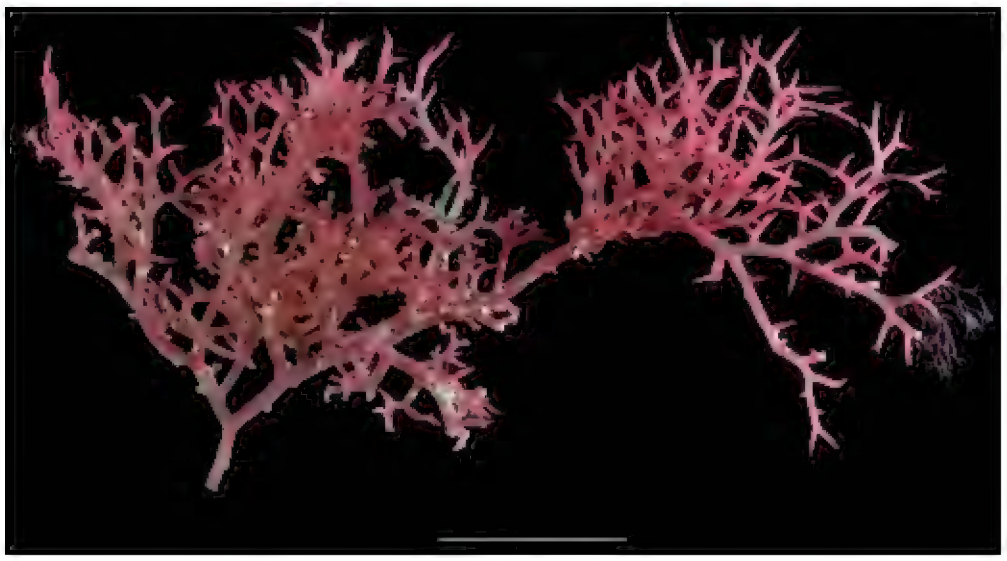

FIGURE 95. *Gracilaria ferox*. DLB7300, live specimen, algal plain seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 5.0 cm.

World Distribution: See Lyra et al. 2016.

Lectotype Locality: Martinique (Oliveira Filho et al. 1983: fig. 3).

Thalli with dense irregular branching are bushy and reach up to 38 cm tall. Axes, 1.0–1.5(–2.0) mm diam. and to 5.0 mm broad, are subterete, compressed to flattened, and irregularly branched. The medulla is 2–5 layered, consisting of cells, 250– 350 µm diam. There is a gradual gradation in cell size outwardly, with outer cortical cells measuring 12–15 µm diam. Cystocarps, 0.75–1.24 mm diam., prominently protrude. Tetrasporangia are immersed in the cortex.

Habitat and Comments: *Gracilaria ferox* occurs mostly in shallow habitats of Puerto Rico. On the basis of overlapping morphological characters, Oliveira Filho et al. (1983) synonymized *G. ferox* with *G. cervicornis*. Lyra et al. (2016), however, reinstated *G. ferox* on the basis of molecular evidence. [Additional illustrations: Cordeiro-Marino 1978: figs. 149–150; Lyra et al. 2021: fig. 11.]

Gracilaria hayi Gurgel, Fredericq et J.N.Norris

FIGURE 96

Gracilaria hayi Gurgel, Fredericq et J.N.Norris 2004a: 178, fig. 7A–F.

Puerto Rican Records: The species is newly reported from Puerto Rico herein. DLBsn, 31.viii.1976, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. (US Alg. Coll. 221486).

West Atlantic Distribution: Panama, United States (North Carolina, Florida), Bermuda, Puerto Rico, Brazil.

Type Locality: Sand plain off Galeta Reef Platform, STRI Galeta Marine Lab., Galeta Point, near Colón, Caribbean Panama.

Thalli are 5.0–10(–15) cm tall above a 1.0–2.0 cm long cylindrical stipe, bearing flat (5–)14–16(–25) mm wide and up to up to 100 µm thick blades. Branching is dichotomous or subdichotomous, and blades terminate in broadly rounded, obtuse apices. Short marginal proliferations may occur. The medulla is

FIGURE 96. *Gracilaria hayi*. DLBsn, herbarium specimen, algal plain seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 2.0 cm.

composed of 3–4(–5) layers of rounded to oval cells, 50–65(–86) µm. Outwardly, a cortex of (1–)2 cell layers is present. The outer cortical layer is of periclinally compressed cells, (6.2–)8–10 × (2.5–)5.0–6.5 µm. Occasional small gland cells are present. Spermatangia are scattered on blade surfaces, in shallow textorii-type sori. Tetrasporangia are scattered across blade surfaces. Hemispherical cystocarps, 1.0–2.0 mm, are scattered on upper surfaces of the main axes.

Habitat and Comments: *Gracilaria hayi* is known only from a single collection in Puerto Rico, from an algal plain at 17 m depth. Gurgel et al. (2004a) noted that in the Caribbean, *G. hayi* had sometimes been referred to as *G. cuneata* and *G. mammillaris*. *Gracilaria hayi* is differentiated by its blade thinness and broad branch apices. Blades of Puerto Rican thalli measured 100 µm thick. [Additional illustrations: Gurgel et al. 2004a: fig. 7A–F; Littler et al. 2008: 115.]

Gracilaria hummii Hommers. et Freshwater

Gracilaria hummii Hommersand et Freshwater 2009: 505–512, figs. 1d–f, 3–5.

Misapplied Names: Gracilaria confervoides sensu Humm 1942, 1944, 1947 [non *Gracilaria confervoides* nom. illeg. (L.) Grev. 1830: liv. 123; *Gracilaria verrucosa* sensu Taylor 1960: 441, pro parte; Schneider and Searles 1991: 328, pro parte [non *Gracilaria verrucosa* (Huds.) Papenfuss 1950: 195, nom. rej.].

Puerto Rican Records: As *Gracilaria confervoides*: Hauck 1888. As *Gracilaria verrucosa*: Taylor, 1960; Almodóvar 1964a, 1964b; Navarro and Almodóvar 1974; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a.

Western Atlantic Distribution: United States (North Carolina), Cuba, Puerto Rico, U.S. Virgin Islands, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: North shore of Shackleford Banks across from Middle Marsh, Back Sound, Carteret County, North Carolina, USA.

Thalli, attached by a discoid holdfast or unattached and drifting, reach up to 60 cm in length. Axes, 0.5 to 2.0 mm diam., are terete. Branching is alternate or dichotomous, to 4(–5) orders; the ultimate branching orders are often unilateral. The branches are constricted at their origin and taper apically. The axes frequently possess fine lateral branchlets, 0.5 mm diam. and 0.5 cm long. The medulla consists of thin-walled cells, 300–650 µm in diam., that are surrounded by a 2–3-layered subcortex and a 2–3-layered outer cortex. Intercellular spaces are seen in the subcortex. Spermatangia occur in conceptacles, 35 µm diam. and 30 µm deep, that may coalesce. Cystocarps are dome-shaped and broadly ellipsoidal, measuring 0.8 mm wide, 1.0 mm long, and 0.8 mm high. Ovoid carposporangia measure to 38 µm long. Oval tetrasporangia, 22–38 µm diam. and 30–45 µm long, originate in the subcortex. Algae are straw colored or pink to dark red in color.

Habitat and Comments: *Gracilaria hummii* is a new record for Puerto Rico based on specimens determined by M. H. Hommersand from Punta Arenas, Mayagüez, collected by M. Yoshizaki, 16.iii.1973 (NCU-A-0014024, Macroalgal Herbarium Portal, https://macroalgae.org/portal/). "*Gracilaria confervoides*" was the name used for the agarophyte harvested in North Carolina (Humm 1942; Schneider and Searles 1991; Hommersand and Freshwater 2009). [Illustration: as *Gracilaria verrucosa*, Taylor 1960: pl. 56: fig. 2.]

FIGURE 97. *Gracilaria isabellana*. DLB4735, herbarium specimen, dredged, offshore from Punta Aguyerada (northern coast). Scale bar = 2.0 cm.

Gracilaria isabellana Gurgel, Fredericq et J.N.Norris

FIGURE 97

Gracilaria isabellana Gurgel, Fredericq et J.N.Norris 2004a: 384, figs. 34–42.
Basionym: *Fucus lacinulatus* M.Vahl 1802: 39.
Homotypic Synonym: Gracilaria lacinulata (M.Vahl) M.Howe 1920b 562.
Puerto Rican Records: As *Gracilaria isabellana*: Ballantine et al. 2016b. As *Gracilaria lacinulata*: Ballantine and Aponte 1997a, 2002a.
Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina), Cuba, Puerto Rico, Brazil, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: St. Croix, U.S. Virgin Islands.
Lectotype: Fucus lacinatus M.Vahl specimen (Copenhagen) illustration in Børgesen 1920: 37, fig. 366 (Gurgel et al. 2004b).

Thalli possess erect axes, up to 12 cm long, to 1.8 cm wide, and to 1.4 mm thick. From a short terete stipe, the compressed axes are linear or lanceolate. Main axial branching is simple, irregular, or di- to trichotomously in one plane. Simple branchlets, originating irregularly, are cut off from the blade margins. Branchlets may be secund and are mostly present distally. Structurally, there is a central medulla of thick-walled cells, 200–520 µm diam., surrounded by a 1–2-layered subcortex of elongated cells, 7.5–18.5 µm diam. and 12–32 µm long, in anticlinal series and a 1–2-layered peripheral cortex of smaller cells. Spherical cystocarps, 1.0–1.1 mm diam. and 675–875 µm high, protrude from both blade surfaces. Male gametophytes and tetrasporophytes are unknown. Algae are yellow green and olive green to dark brown in color.

Habitat and Comments: *Gracilaria isabellana* is known from the lower intertidal to shallow subtidal, frequently in wave-exposed habitats. The species displays a wide range morphological variation. [Additional illustration: as *Fucus lacinatus*, Børgesen 1920: fig. 366.]

Gracilaria mammillaris (Mont.) M.Howe

FIGURE 98

Gracilaria mammillaris (Mont.) M.Howe 1918a: 515.

Basionym: *Rhodymenia mammillaris* Mont. 1842: 252 [Montagne 1842].

Puerto Rican Records: As *Rhodymenia mammillaris*: Hauck 1888. As *Gracilaria mammillaris*: Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1962, 1964a, 1964b, 1965; Díaz-Piferrer and Caballer de Pérez 1964; Navarro and Almodóvar 1974; Ortiz Sotomayor 1976; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: United States (North Carolina, Florida), Bermuda, Barbados, Belize, Cuba, El Salvador, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Panama, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Martinique, French West Indies.

Thalli possess several axes originating from a common holdfast that reach 5.0–10(–15) cm tall. The axes are subterete below, expanding above, where they become flattened, 3.0–5.0(–10) mm broad and 250–330 µm thick. The axes are fleshy to leathery in texture, have obtuse apices, and are irregularly dichotomously branched with rounded sinuses. A central 4–5-layered medulla consists of thick-walled cells, 50–170 µm diam., and is surrounded by a 1–2-layered cortex of ovoid cells, 4.0–7.0 µm diam. and 6.0–18 µm long. Spermatangia occur in small surface sori. Hemispherical cystocarps, 1.3 mm diam., are scattered over the blade. Spherical carposporangia measure to 30 µm diam. Tetrasporangia, borne within the cortex, measure 25–35 µm diam. Algae are dull to bright red in color.

Habitat and Comments: *Gracilaria mammillaris* is commonly found in shallow water and growing on exposed rocks. Hardesty and Freshwater (2018) reported that on the basis of *rbc*L sequences, none of the specimens identified as *G. mammillaris* from offshore habitats in North Carolina corresponded to that species but, rather, four separate species. This suggests Puerto Rican specimens identified as "*G. mammillaris*" should be critically studied. [Additional illustrations: Taylor 1960: pl. 59: fig. 4; Núñez-Resendiz et al. 2019b: figs. 44, 45; Lyra et al. 2021: fig. 14.]

FIGURE 98. *Gracilaria mammillaris*. DLB3992, herbarium specimen, Islote, Arecibo, 10–12 m. Scale bar = 1.0 cm.

Gracilaria tikvahiae McLachlan

FIGURE 99

Gracilaria tikvahiae McLachlan 1979: 19, fig. 1.

Heterotypic Synonyms: Gracilaria multipartita var. *angustissima* Harvey 1853: 107.

Misapplied Name: Gracilaria foliifera sensu Taylor 1960: 446–447, pro parte [non *Gracilaria foliifera* (Forrsk.) Børgesen 1932: 7].

Puerto Rican Records: As *Gracilaria multipartita* var. *angustissima*: Hauck 1888. As *Gracilaria foliifera*: Díaz-Piferrer 1963; Almodóvar 1964a, 1964b; Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar 1965; Navarro and Almodóvar 1974; Ortiz Sotomayor 1976; Almodóvar and Ballantine

FIGURE 99. *Gracilaria tikvahiae*. DLB3373, herbarium specimen, algal plain, 1.5 km seaward Media Luna Reef, La Parguera. Scale bar = 2.0 cm.

1983. As *Gracilaria tikvahiae*: Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Belize, Caribbean Mexico, United States (North Carolina, Georgia, Florida), Bermuda, Bahamas, Barbados, Grenadines, Hispaniola, Jamaica, Martinique, Panama, Puerto Rico, Turks and Caicos, Brazil, Colombia, Uruguay, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Barrachois Harbour, Colchester Co., Nova Scotia, Canada.

Thalli reach up to 10–30 cm in height. Lower axes slender, becoming thicker and subterete to compressed, measuring 2.0–15 mm or more in width above. Branching, in one plane, is di-trichotomous or alternate, with marginal branching from the laciniate axes. Proliferations and ultimate branches usually filiform. The medulla, composed of cells 70–270 µm diam., grades abruptly into the 1–4-layered cortex. The peripheral cortical cells measure 5.0–13 µm diam. Cystocarps, to 1.0 mm diam., prominently project from the faces or margins of the bearing blades. Oval to spherical carposporangia measure 15–40 µm diam. Spermatangia not found in Puerto Rican specimens. Ovoid tetrasporangia, 10–35 µm diam. and 20–45 µm long, occur in the outer cortex. Algae are variable in color, frequently greenish to dull purple.

Habitat and Comments: In Puerto Rico *Gracilaria tikvahiae* typically occurs in shallow embayments down to 20 m depths (Ortiz Sotomayor 1976, as *G. foliifera*). Historically, a number of phycologists have commented on the similarities between *G. foliifera* and *G. tikvahiae*, and earlier reports of Puerto Rican algae followed Taylor (1960) and referred this alga to "*Gracilaria foliifera.*" Nevertheless, McLachlan and Edelstein (1977) pointed to differences in gonimoblast details between the species, and Guiry and Freamhainn (1986) concluded that *G. foliifera* is not present on the North American Atlantic coast and that *G. tikvahiae* is distributed from Nova Scotia to the Caribbean. [Additional illustrations: as *Gracilaria foliifera*, Taylor 1960: pl. 55: fig. 1; as *Gracilaria tikvahiae*, McLachlan 1979: fig. 1; Littler and Littler 2008: 116.]

Excluded Taxa

***Gracilaria curtissiae* J.Agardh 1885: 61.**

Puerto Rican records have followed Díaz-Piferrer's (1963) report. Ortiz Sotomayor (1976) considered *G. curtissiae* to be a doubtful record for Puerto Rico and annotated a number of herbarium specimens from the island as *G. cuneata*. Our examination of a Díaz-Piferrer Puerto Rican specimen identified as *G. curtissiae* (US Alg. Coll. 094633) led to our assignment of that specimen to *Gracilaria cearensis*.

***Gracilaria dura* (C.Agardh) J.Agardh 1842: 151.**

Gracilaria dura was reported from Fajardo, Puerto Rico, by Hauck (1888). The species was treated as an uncertain record by Taylor (1960), and as the species has not been re-collected and specimens have not been located, we do not recognize that the species occurs in Puerto Rico.

***Gracilaria foliifera* (Forssk.) Børgesen 1932: 7.**

Puerto Rican records by Ortiz Sotomayor 1976 (as "*Gracilaria foliifer*") and, as *Gracilaria foliifera*, by Taylor (1960), Almodóvar (1962), and Almodóvar and Ballantine (1983) are excluded from the Puerto Rican algal flora. *Gracilaria foliifera* is currently not known to occur in the Atlantic Ocean (Guiry and Freamhainn 1986; Silva et al. 1996).

***Gracilaria wrightii* (Turner) J.Agardh 1852: 599.**

Gracilaria wrightii was reported from Manati, Puerto Rico, by Hauck (1888). As the species has not been re-collected and specimens have not been located, we do not recognize that the species occurs in Puerto Rico. Further, the basionym *Fucus wrightii* Turner (1811: 32) has two syntype localities, Red Sea and West Indies, and a lectotype needs to be chosen to resolve the taxonomic status of the taxon (Guiry and Guiry 2024).

Gracilarioideae Tribe Gracilariopsideae Gurgel, J.N.Norris et Fredericq

Gracilariopsis E.Y.Dawson

Gracilariopsis E.Y.Dawson 1949: 40.

Terete axes are short to very long, some can be up to 2 m in length, and are irregularly or alternately branched, sparsely to several orders. Gametophytes are dioecious. Spermatangia originate in sori in the outer cortex. The female gametophyte support cell is cut off from inner cortical cells and bears a 2-celled carpogonial branch. Carposporangia are cut off terminally in chains by gonimoblast filaments. Cruciately divided tetrasporangia are cut off by inner cortical cells.

Most species are morphologically similar to other cylindrical species of *Gracilaria* and can be separated only by gametophytic reproductive structures (Fredericq and Hommersand 1989; Gurgel et al. 2018). One of the 25 recognized *Gracilariopsis* species occurs in Puerto Rico. *Gracilariopsis carolinensis* is included in the key to Puerto Rican *Gracilaria* and *Gracilariopsis* above.

Gracilariopsis carolinensis L.M.Liao et Hommers.

FIGURE 100

Gracilariopsis carolinensis L.M.Liao et Hommers. in Gurgel et al. 2003: 163, figs. 3c, 6.

Misapplied Names: Gracilaria sjoestedtii sensu Taylor 1960: 449 pro parte [non *Gracilaria sjoestedtii* Kylin 1930: 55]; *Gracilariopsis tenuifrons* (C.J.Bird et E.C.Oliveira) Fredericq et Hommers. 1989: 240.

Puerto Rican Records: As *Gracilaria sjoestedtia*: Almodóvar and Blomquist 1961. As *Gracilaria sjoestedtii*: Almodóvar 1964a,

FIGURE 100. *Gracilariopsis carolinensis*. DLBsn, herbarium specimen, Ballena Bay, Guánica. Scale bar = 2.0 cm.

1964b; Díaz-Piferrer and Caballer de Pérez 1964; Navarro and Almodóvar 1974; Ortiz Sotomayor 1976; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997. As *Gracilariopsis tenuifrons*: Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: United States (North Carolina, South Carolina, Florida), Cuba, Martinique, Puerto Rico.

Type Locality: Kure Beach, Fort Fisher, New Hanover Co., North Carolina, USA.

Thalli reach up to 2.0 m in height. The attenuate, terete axes, 0.5–2.0 mm diam., are sparsely radially branched to several degrees. The cortex consists of 4–6 layers of small cells. Spermatangia are in open, superficial sori. Cystocarps are dome shaped. Carpogonia are borne in terminal chains from gonimoblast filaments. Ellipsoid to subglobose tetrasporangia, 25–28 µm diam. and 33–48 µm long, are scattered in the outer cortex. Algae are purplish to brownish or red in color.

Habitat and Comments: *Gracilariopsis carolinensis* has been widely reported as "*Gracilaria sjoestedtii*." Gurgel and Fredericq (2004) recognized *Gracilariopsis sjoestedtii* (Kylin) E.Y.Dawson (1949) to be a synonym of *Gracilariopsis andersonii* (Grunow) E.Y.Dawson (1949; type locality Santa Cruz, California) and reported *Gracilariopsis andersonii* was restricted to the eastern Pacific. [Additional illustrations: as *Gracilariopsis sjoestedtii*, Joly et al. 1963: pl. 3; as *Gracilariopsis carolinensis*, Gurgel et al. 2003: figs. 3c, 6; Littler et al. 2008: 117.]

Halymeniales G.W.Saunders et Kraft

Halymeniaceae Bory

Corynomorpha J.Agardh

Corynomorpha J.Agardh 1872: 3, nom. cons.

Erect thalli are terete to clavate. Branching is simple or dichotomous. Thalli are cartilaginous in texture. Structurally, algae are multiaxial, with anastomosing filaments comprising the medulla that are surrounded by a several-layered pseudoparenchymatous cortex. The outermost cortical cells are in anticlinal rows. The genus displays an isomorphic alternation of generations. Reproductive structures occur in nemathecia. Spermatangia occur in chains. Cystocarps are immersed within nemathecia. Cruciately or irregularly divided tetrasporangia are cut off laterally by nemathecial filaments. One of the two recognized *Corynomorpha* species occurs in Puerto Rico.

Corynomorpha clavata (Harv.) J.Agardh

Corynomorpha clavata (Harv.) J.Agardh 1872: 4.

Basionym: *Acrotylus clavatus* Harv. 1853: 196.

Puerto Rican Records: The species is newly reported from Puerto Rico herein. Its occurrence is based on specimens collected by B. Brooks at three sites, 26 to 30 m depth, northwest Culebra Island, Puerto Rico. Specimens are deposited in US Alg. Coll., D&ML30310 (US Alg. Coll. 227928), D&ML41368 (US Alg. Coll. 228377), D&ML41437 (US Alg. Coll. 228362).

Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Bermuda, Cuba, Guadeloupe, Puerto Rico, Brazil, Colombia.

Type Locality: Key West, Florida, USA.

Thalli are club shaped to terete and measure 3.0–8.0 mm diam. and 2.0–6.5 cm long, with obtuse apices. Borne on infrequently branched stipes, 2.0–5.0 mm long, algae are cartilaginous to firmly fleshy in texture. Medullary filaments, averaging ~7.5 µm diam., occur centrally within a mucilaginous gel and give rise to a cortex of radially organized rows of cells. Surface cells measure 3.0–5.0 µm diam. Cystocarps are borne distally and are immersed. Algae are dull purple red in color.

Habitat and Comments: In Puerto Rico *Corynomorpha clavata* is not common and, when encountered, is frequently solitary. Although Almodóvar (1970) had reported "*Corynomorpha clavata*," that specimen was later found to be misidentified, and a new species, *Botryocladia wynnei* D.L.Ballant. (1985) was described to account for the Puerto Rican entity. [Illustrations: Taylor 1960: pl. 64: fig. 3; Littler and Littler 2000: 73.]

Cryptonemia J.Agardh

Cryptonemia J.Agardh 1842:100.

Thalli possess flat blades above a stipe. The blades, simple or palmately to dichotomously branched, are variously shaped, being linear-lanceolate to broadly lobed. Blades are entire, proliferous, or laciniate. Blades of some species possess midribs. Structurally, there is a filamentous medulla with stellate cells surrounded by a multilayered cortex. The outer cortical cells are in anticlinal rows. Reproduction involves an isomorphic alternation of generations. Algae are dioecious, with spermatangia occurring in large sori. Carpogonial branches are 2-celled and are borne in cortical fascicles of cells called ampullae. Auxiliary cells occur in separate ampullae. Cystocarps possess a carpostome. Cruciately divided tetrasporangia are scattered in the cortex. Fifty-one species of *Cryptonemia* are recognized worldwide; five of these occur in Puerto Rico.

KEY TO THE *CRYPTONEMIA* SPECIES OF PUERTO RICO

1. Thalli with a midrib . . . . . *C. seminervis*
   Thalli without a midrib 2
2. Blades are briefly stipitate, dentate . . . . . *C. crenulata*
   Blades stipitate, not dentate or subdentate 3
3. Blades lanceolate to oblanceolate . . . . . *C. bengryi*
   Thalli are broad bladed 4
4. Thalli frequently with multiple, generally deeply lobed blades . . . . . *C. bermudensis*
   Thalli generally comprise single non-dissected blades . . . . . *C. floridana*

Cryptonemia bengryi W.R.Taylor

FIGURE 101

Cryptonemia bengryi W.R.Taylor 1960: 427, 633, 822, pl. 80: fig. 1.

Puerto Rican Records: Díaz-Piferrer 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a.

Western Atlantic Distribution: Jamaica, Panama, Puerto Rico, Trinidad and Tobago, Brazil, Venezuela.

Type Locality: Alligator Pond Bay, Manchester, Jamaica.

Thalli reach up to 14 cm in height. Several terete, alternately radially branched stipes, 1.0–5.0 cm long, issue from a common holdfast. The stipes bear ecostate blades, 2.0–8.0 cm long, 10–15 mm broad, and 100–195 µm thick. The blades, irregularly lanceolate to oblanceolate, are frequently subpalmately divided. Blade margins are thickened and entire or subdentate. Structurally, the medulla consists of filaments, 2.5–6.6 µm diam. Stellate ganglia, ~8.5 µm diam., with up to 7 arms, are present but not abundant. A 2-layered subcortex of transversely oval cells and a 1-cell layer outer cortex of thick-walled cells, 5.0–8.5 µm diam., surrounds the medulla. Reproduction is unknown. Algae are dull to sub-nitent and wine red in color.

Habitat and Comments: In Puerto Rico, *Cryptonemia bengryi* is known from one locale, exclusively in shallow water at Yabucoa Bay. [Additional illustration: Taylor 1960: pl. 80: fig. 1.]

Cryptonemia bermudensis (Collins et M.Howe) C.W.Schneid., C.E.Lane et G.W.Saunders

Cryptonemia bermudensis (Collins et M.Howe) C.W.Schneid., C.E.Lane et G.W.Saunders 2018: 362, figs. 16, 17.

Basionym: *Halymenia bermudensis* Collins et M.Howe 1916: 169.

Puerto Rican Records: As *Halymenia bermudensis*: Ballantine and Aponte 1997a, 1997b.

Western Atlantic Distribution: United States (North Carolina, Florida), Bermuda, Puerto Rico, Brazil.

Type Locality: Castle Harbour, near Tucker's Town, Bermuda.

Thallus blades are borne by branched terete stipes, 450–750 µm diam. and to 1.0 cm long. The stipes extend briefly into the blades. The membranous blades are suborbicular or obovate when young, becoming deeply lobed. The blades are firm or slightly gelatinous, 60–120 µm thick and 4–30 cm wide, and possess rounded obtuse apices. Subentire or lobed margins of the blade are ruffled and sinuate-crenate. The medulla is moderately compact, composed of cells, 3.0–8.0 µm diam., interspersed with larger-diameter cells, 6.0–20 µm diam. Within the medulla are substellate ganglia, 15–65 µm diam. Surrounding the medulla is a 1–3-layered subcortex of cells, 13–25 µm diam. The outer cortex is 1–3 cells thick; surface cortical cells measure 5.0–10 µm diam. Female gametophytes are unknown. Tetrasporangia

FIGURE 101. *Cryptonemia bengryi*. DLBsn, herbarium specimen, Yabucoa Bay, <1.0 m. Scale bar = 2.0 cm.

measure 8.0–10 µm diam. and 12–26 µm long. Algae are violet red in color.

Habitat and Comments: In Puerto Rico, the species is recognized on the basis of a single specimen collected at 17 m depth at Media Luna Reef. The Puerto Rican specimen possessed somewhat smaller dimensions than those reported for Bermuda thalli that occurred in shallower-water habitats (Schneider et al. 2018). Guimarães and Fujii (1999) considered that *Cryptonemia bermudensis* (as *Halymenia bermudensis*) was conspecific with *Cryptonemia floridana* (as *Halymenia floridana*). However, Schneider et al. (2018) maintained them as separate entities on molecular bases.

Cryptonemia crenulata (J.Agardh) J.Agardh

FIGURE 102

Cryptonemia crenulata (J.Agardh) J.Agardh 1851: 225–226.

Basionym: *Phyllophora crenulata* J.Agardh 1841: 18.

Puerto Rican Records: As *Cryptonemia crenulata*: Hauck 1888; Taylor 1960; Almodóvar 1964a, 1965; Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a; Ballantine et al. 2016b.

Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina, Florida), Bermuda, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Bahia, Brazil.

Thalli are briefly stipitate and reach to 15 cm in height. Strap-shaped blades, 0.2–1.5 cm broad and 60–150 µm thick, lack midribs. Axes are dichotomously or palmately branched. Blade margins are crisped, undulate, and dentate. The marginal teeth are frequently divided. Structurally, thalli possess a

FIGURE 102. *Cryptonemia crenulata*. In situ photograph, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Field = 15 cm.

filamentous medulla with stellate ganglia, with filaments 2.0–10 µm diam. The cortex is 1–3 cell layers with inner cortical cells, 10–30 µm diam., and peripheral cortical cells, 5.0–7.0 µm diam. Distally situated tetrasporangia measure 8.0–10 µm diam. and 10–13 µm long.

Habitat and Comments: *Cryptonemia crenulata* occurs in a variety of habitats and is known from shallow to deep water (82 m) in Puerto Rico; it is particularly common at the offshore algal plains. Schneider et al. (2018) attributed specimens previously referred to *C. crenulata* from Bermuda to be their new species *C. antricola* C.W.Schneid., C.E.Lane et G.W.Saunders. The latter species differs from C. *crenulata* in lacking a crenulate margin. [Additional illustration: Taylor 1960: pl. 58: fig. 4.]

Cryptonemia floridana (J.Agardh) J.P.Soares, T.Sauvage et M.T.Fujii

FIGURE 103

Cryptonemia floridana (J.Agardh) J.P.Soares, T.Sauvage et M.T.Fujii 2024: 3, figs. 3–32.

Basionym: *Halymenia floridana* J.Agardh 1892: 59.

Heterotypic Synonym: Halymenia gelinaria Collins et M.Howe 1916: 173.

Puerto Rican Records: As *Halymenia gelinaria*: Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a.

Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina, Florida), Bermuda, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Florida, USA.

Thalli possess membranous blades, 5.0–20 cm in height and 4.0–10 cm wide, that are borne on slender stipes a few mm long. The highly gelatinous blades, 60–550 µm thick, are roundish when young, becoming oval and lobed. Margins are generally entire, with blades possessing obtuse apices. Loose to dense medullary filaments, 3.0–14 µm diam., frequently anastomose to form stellate ganglia, 15–65 µm diam. The ganglia possess 3–10 arms. A 1–3-layered cortex surrounds the medulla, with cortical cells measuring 7.0–8.5 µm diam. Gametophytes are dioecious. Spermatangia occur in surface sori. Globose cystocarps, 100–250 µm diam., are immersed and appear as swellings on the

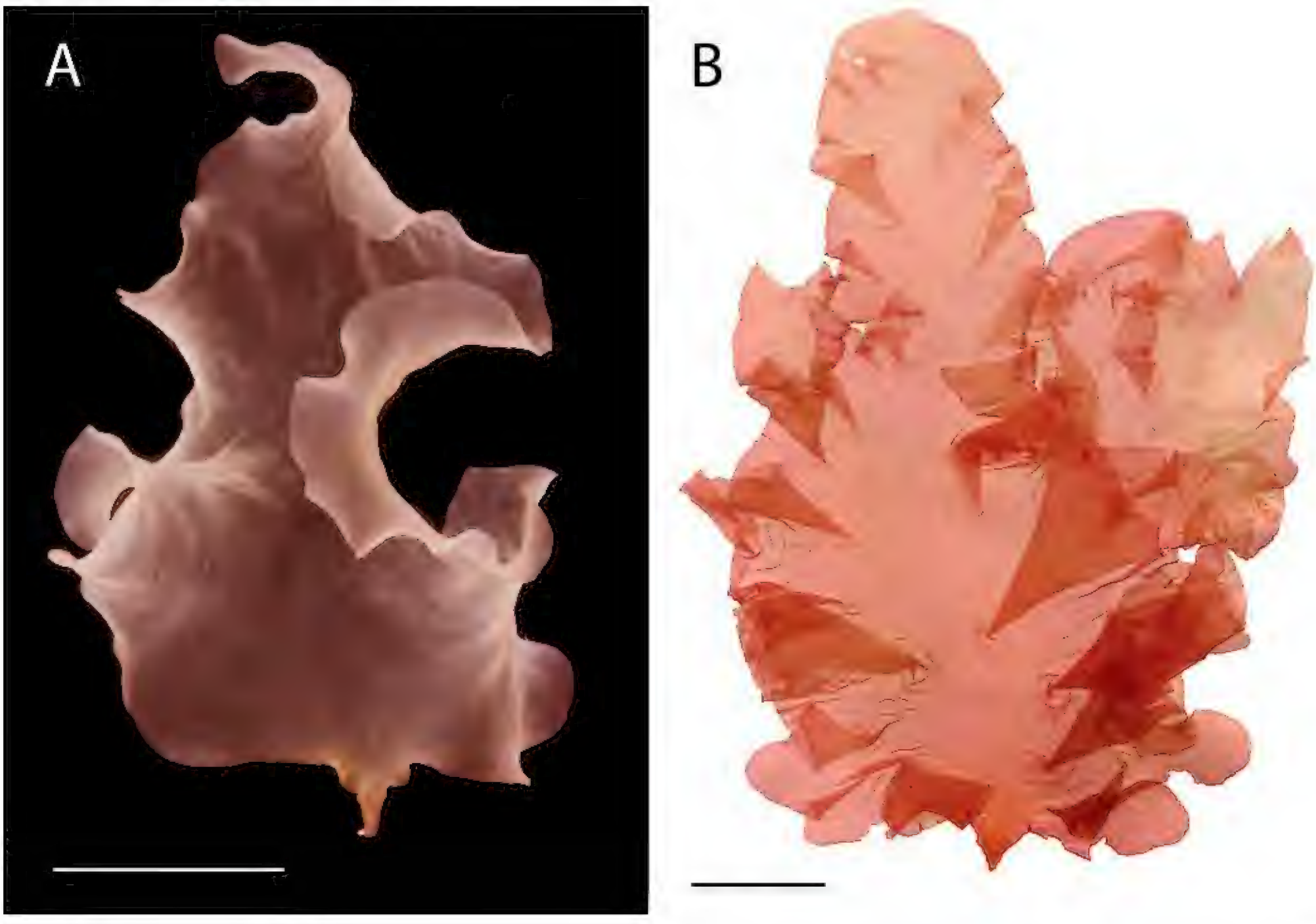

FIGURE 103. *Cryptonemia floridana*. (A) DLBsn, live specimen, algal plain, offshore from Punta Brea, 17 m. Scale bar = 5.0 cm. (B) DLBsn, herbarium specimen, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 5.0 cm.

surface. Carposporangia measure 4.0–8.0 µm diam. Ovoid tetrasporangia, 8.0–13 µm diam. and 12–26 µm long, are scattered in the outer cortex. Algae are rose or purplish in color.

Habitat and Comments: *Halymenia floridana* is not frequently encountered in Puerto Rico, having been collected at the offshore algal plains on the southern coast of Puerto Rico. Although Littler et al. (2008) treat *H. gelinaria* as separate from *H. floridana*, Guiry and Guiry (2024) treat the former as a synonym of *H. floridana*. [Additional illustrations: Taylor 1960: pl. 53: fig. 2; Littler and Littler 2000: 107.]

Cryptonemia seminervis (C.Agardh) J.Agardh

FIGURE 104

Cryptonemia seminervis (C.Agardh) J.Agardh 1846: [v], pl. 17.

Basionym: Sphaerococcus seminervis C.Agardh 1821: [iv], pl. 17.

Heterotypic Synonym: Cryptonemia luxurians (C.Agardh) J.Agardh 1851: 228.

Puerto Rican Records: As *Cryptonemia luxurians*: Taylor 1960; Almodóvar and Blomquist 1965; Díaz-Piferrer 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a.

Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina, Florida), Bermuda, Barbados, Cuba, Grenadines, Guadeloupe, Hispaniola, Martinique, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela, Argentina.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Cádiz, Spain.

FIGURE 104. *Cryptonemia seminervis*. MDP3246, herbarium specimen, Yabucoa Bay. Scale bar = 2.0 cm.

Thalli reach to 25 cm in height. The stipe, 1.0–1.5 mm long, extends into the blades as a midrib for some distance. Thalli are denuded and subterete below and alate above. Branching is 3–7 times subdichotomous to palmate, and the branches are linear-oblong, 5.0–15(–20) mm wide and 100–200 µm thick. Blade margins are undulate and frequently possess proliferations. Medullary filaments, 2.0–8.0 µm diam., are compact. Inner cells of the 1–2-layered cortex measure 10–25 µm diam., and peripheral cortical cells measure 5.0–7.0 µm diam. Gametophytes are dioecious. Spermatangia are borne in marginal blades. Spherical carposporophytes, 100–150 µm diam., are located in marginal branchlets or blade apices. Ovoid tetrasporangia, 7.0–10 µm diam. and 10–13 µm long, occur in small marginal branchlets.

Habitat and Comments: *Cryptonemia seminervis* has long been referred to as *C. luxurians* in the western Atlantic, until Price et al. (1986) considered the two synonymous, an interpretation followed by Dawes and Mathieson (2008) and Guiry and Guiry (2024). Nevertheless, the taxonomic status of Caribbean *C. seminervis* is not resolved. On the basis of their molecular analysis, Yang and Kim (2014) maintained *C. seminervis* from Spain and *C. luxurians* from Brazil as separate species. They also demonstrated *rbc*L sequence identity between the type species of *Cryptonemia lomation* (Bertoloni) J.Agardh and *C. seminervis*, a relationship previously suggested by Athanasiadis (1987). Recently, *C. lomation* has been considered to be a synonym of *C. palmetta* (S.G.Gmelin) Woelkerling, G.Furnari, Cormaci et McNeill (2019). Further phylogenetic analyses of Caribbean *Cryptonemia luxurians*, *C. seminervis*, and *C. palmetta* are needed to clarify their nomenclature and taxonomic status. [Additional illustration: as *C. luxurians*, Taylor 1960: pl. 58: fig. 3.]

Grateloupiaceae F.Schmitz

Dermocorynus P.Crouan et H.Crouan

Dermocorynus P.Crouan et H.Crouan 1858: 70.

Thalli possess a basal mucilaginous crust, bearing erect papillae or simple branched fronds. Gametophytes are monoecious. Female gametophytes possess a carpogonial branch variously reported as 2-celled (S. C. Lindstrom and J. A. Lewis in Guiry and Guiry 2024) and 5-celled (Gargiulo et al., 2013: 29)

and a 4-celled auxiliary cell branch borne on an ampullary filament. Gonimoblasts develop outwardly, forming 2 or more lobes surrounded by involucral filaments. Spermatangia are produced singly or in pairs by cortical cells. Tetrasporocytes, tetrahedrally or irregularly divided, occur in surface papillae. Of four currently recognized *Dermocorynus* species, there is a single species in Puerto Rico.

Dermocorynus dichotomus (J.Agardh) Gargiulo, Morabito et Manghisi

FIGURE 105

Dermocorynus dichotomus (J.Agardh) Gargiulo, Morabito et Manghisi 2013: 31, figs. 25–35 (as *dichotoma*).

Basionym: *Grateloupia dichotoma* J.Agardh 1842: 103.

Puerto Rican Records: As *Grateloupia dichotoma* sensu Taylor 1960: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a.

Western Atlantic Distribution: Costa Rica, Caribbean Mexico, Guadeloupe, Jamaica, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Syntype Localities: "Ad littora Galloprovinciae et Niceam," probably Golfe de Saint-Hospice near Nice, France (fide Index Nominum Algarum 2024).

Thalli originate from basal disks and reach 3.0–7.0 cm in height. Strap-shaped compressed blades, 3.0–5.0 mm wide and 120–250 µm thick, are borne on short stipes. The blades are simple proximally and dichotomously or irregularly branched distally. Marginal proliferations are commonly produced. Carpogonial branches are 5-celled; cystocarps, ~180 µm diam., occur in small groups. Tetrasporangia, 14 µm diam., are embedded in the cortex and scattered. Algae are reddish to blackish purple in color.

Habitat and Comments: In Puerto Rico, *Dermocorynus dichotomus* has been collected intertidally on the north coast. Gargiulo et al. (2013) reinstated the genus *Dermocorynus* on molecular bases and made the combination *D. dichotomus* (J.Agardh) Gargiulo, Morabito et Manghisi. Soares et al. (2018) followed the opinion of Azevedo (2016) that Brazilian species assigned to *Grateloupia dichotoma* were probably a new species. [Additional illustrations: as *Grateloupia dichotoma*, Cordeiro-Marino 1978: figs. 140–142; as *Dermocorynus dichotomus*, Cormaci et al. 2021: pl. 3: figs. 4, 5.]

FIGURE 105. *Dermocorynus dichotomus*. MDP609, herbarium specimen, front of Fortaleza, San Juan. Scale bar = X.0 cm.

Grateloupia C.Agardh

Grateloupia C.Agardh 1822: 221, nom. cons.

Thalli, borne on stipes, are membranous to foliaceous. Lubricous blades are linear to lanceolate and are branched dichotomously or pinnately in one or more planes. Structurally, thalli possess a filamentous medulla surrounded by an inner cortex of anastomosing stellate cells and an outer cortex of anticlinal files of cells. Reproduction involves an isomorphic alternation of generations. Spermatangia occur in nemathecia borne on the surface. Female reproductive structures occur in sparingly branched ampullae. Carpogonial branches are 2-celled, and auxiliary cells occur in separate ampullae. Cystocarps are embedded in female thallus tissue. Cruciate tetrasporangia are cut off in an intermediate cortical layer. There are three *Grateloupia* species in Puerto Rico of 98 species recognized worldwide.

KEY TO THE *GRATELOUPIA* AND *PHYLLYMENIA* SPECIES OF PUERTO RICO

1. Thalli much branched, branching pinnate or radial; distal branches terete . . . . . ***G. filicina* sensu Taylor**
   Thalli sparingly branched 2
2. Blades marginally pinnate, 240–950 µm thick; bases symmetrical . . . . . ***Phyllymenia gibbesii***
   Blade margins undulate, sometimes lacerate, 160–250 µm thick; bases asymmetrical . . . . . ***G. cuneifolia***

Grateloupia cuneifolia J.Agardh

FIGURE 106

Grateloupia cuneifolia J.Agardh 1849: 85.

Puerto Rican Records: Almodóvar 1964a, 1965; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: United States (Florida), Jamaica, Martinique, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela, Uruguay.

World Distribution: See Guiry and Guiry 2024.

Type Locality: La Guayra, Venezuela.

Thalli reach to 40 cm in height. The short stipes expand into foliaceous lanceolate or oval blades, 4.0–5.0 cm wide and 160–250 µm thick. Blade margins are smooth to dentate and frequently have proliferations. Medullary filaments measure 1.0–3.0 µm diam. The cortex is 3–7-layered, with peripheral cells measuring 2.0–4.0 µm diam. Ovoid tetrasporangia, 8.0–19 µm diam. and 26–35 µm long, are scattered and situated in the inner cortex. Spherical cystocarps measure to 130 µm diam., and carposporangia are 8.0–14 µm diam. Algae are purple or greenish in color.

Habitat and Comments: In Puerto Rico, *Grateloupia cuneifolia* has been most commonly collected at Yabucoa Bay (southeast Puerto Rico) in shallow water. [Additional illustrations: Taylor 1960: pl. 54: fig. 4; Cordeiro-Marino 1978: figs. 135–139.]

FIGURE 106. *Grateloupia cuneifolia.* DLB2184, herbarium specimen, Yabucoa Bay, intertidal. Scale bar = 5.0 cm.

Grateloupia filicina sensu Taylor

FIGURE 107

Grateloupia filicina sensu Taylor 1960: 424, pl. 54: figs. 2, 3 [non *Grateloupia filicina* (J.V.Lamour.) C.Agardh 1822: 223].

Puerto Rican Records: Hauck 1888; Taylor 1960; Almodóvar 1964a, 1964b, 1965; Díaz-Piferrer and Caballer de Pérez 1964; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a.

Western Atlantic Distribution: Panama, United States (Florida, Georgia, North Carolina, South Carolina), Bahamas, Belize, Costa Rica, Cuba, Dominica, El Salvador, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Uruguay, Argentina.

FIGURE 107. *Grateloupia filicina.* DLB2182, herbarium specimen, Yabucoa Bay. Scale bar = 2.0 cm.

World Distribution: See Guiry and Guiry 2024.
Type Locality: Trieste, Italy.

Compressed to flattened thalli reach 75 cm in height, 2.0–5.0 mm in width, and 120–200 µm thick. Algae possess discoid holdfasts and have a brief stipe proximally. Thalli are firmly gelatinous in texture. Axes increase in width from their bases and taper distally. Branching is typically pinnate and sometimes proliferous from the blade surfaces. The medulla is composed of loosely placed filaments that measure 3.0–7.0 µm diam. The cortex consists of branched files of cells, with surface cells measuring 3.0–5.0 µm diam. Gametophytes are monoecious. Spermatangia develop from peripheral cortical cells. Cystocarps, 150–260 µm diam., are immersed. Carposporangia measure 7.5–15(–21) µm diam. Ellipsoidal tetrasporangia, cut off by inner cortical cells in marginal branchlets, measure 11–27 µm diam. and 25–47 µm long. Algae are dark purplish brown in color.

Habitat and Comments: The entity referred to *Grateloupia filicina* is found growing on rocks and seawalls intertidally and in shallow-water protected environments in Puerto Rico. De Clerck et al. (2005a) conducted a molecular study of geographically disjunct populations referred to *G. filicina* and found a number of divergent clades, concluding that *Grateloupia filicina* is restricted to the Mediterranean. *Grateloupia pennulata* (Pöppig) Kütz. is listed in Guiry and Guiry (2024) as a synonym of *G. filicina* despite the fact that *G. pennulata* has a type locality in Cuba (De Clerck et al. 2005a: 392) and that *G. filicina* is no longer considered to be a member of the Caribbean flora. Whether or not Puerto Rican *Grateloupia filicina* sensu Taylor (1960) is actually conspecific with *G. pennulata* remains an open question. [Additional illustrations: Børgesen 1935: pls. 7–9; Cordeiro-Marino 1978: figs. 143–145; Schneider and Searles 1991: figs. 325–326; Littler et al. 2008: 121; Braune and Guiry 2011: fig. 183.2; Gargiulo et al. 2013: figs. 1–12.]

Excluded Taxon

***Grateloupia doryphora* (Mont.) M.Howe 1914: 169.**

The report of *Grateloupia doryphora* from Puerto Rico by Ballantine and Aponte (1997a) is probably based on a misidentification. Gavio and Fredericq (2002) indicated that the species is probably limited to Peru and Chile and the populations from Rhode Island, New York, Brittany (France), and England reported in the literature as *G. 'doryphora'* have been misidentified.

Phyllymenia J.Agardh

Phyllymenia J.Agardh 1848: 47.

Thalli are either terete or bladed above a short stipe. Branching may be proliferous from axes' margins. Structurally, thalli have a filamentous medulla surrounded by a cortex of cells that are progressively smaller outwardly. Reproductively, algae possess an alternation of isomorphic generations. Ampullae possess 2 or 3 branching orders. Carpogonial branches are 2-celled, and auxiliary cells are borne in separate ampullae. Cystocarps and tetrasporangia are embedded. On the bases of morphological and genetic analyses, De Clerck et al. (2005b) concluded that *Phyllymenia* was a synonym of *Grateloupia*; however, Gargiulo et al. (2013) reinstated *Phyllymenia*. Eight species of *Phyllymenia* are recognized, one of which is known for Puerto Rico.

Phyllymenia gibbesii (Harv.) S.M.Lin, Rodr.-Prieto, De Clerck et Guiry

FIGURE 108

Phyllymenia gibbesii (Harv.) S.M.Lin, Rodr.-Prieto, De Clerck et Guiry in Rodriguez-Prieto et al. 2022: 243, fig. 6.

Basionym: *Grateloupia gibbesii* Harv. 1853: 199, pl. 26.

Puerto Rican Records: As *Grateloupia gibbesii*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983.

FIGURE 108. *Phyllymenia gibbesii*. MDP3390, herbarium specimen, Playa Cafacoles, Arecibo. Scale bar = 2.0 cm.

Western Atlantic Distribution: Caribbean Mexico, United States (Florida, South Carolina), Jamaica, Martinique, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Sullivan's Island, Charleston, South Carolina, USA.

Membranous thalli reach up to 15–60 cm in height. Linear to lanceolate flattened blades are simple, alternately branched, or pinnate from the margins. The blades are 1.0–5.0 cm broad and 240–950 µm thick. Tangled medullary filaments, 1.0–4.0 µm diam., are embedded within a gelatinous matrix. Surrounding the medulla is a 3–8-layered cortex. The inner cortex cells measure 5.0–10 µm diam., and the peripheral cortical cells measure 2.0–6.0 µm diam. Spermatangia occur in scattered sori and originate from outer cortical cells. Immersed cystocarps, to 150 µm diam., produce carposporangia, 9.0–16 µm diam. Ovoid tetrasporangia, 10–18 µm diam. and 28–45 µm long, occur in marginal branchlets and are cut off in the inner cortex. Immersed cystocarps, to 150 µm diam., produce carposporangia, 9.0–16 µm diam. Algae are red or blackish purple in color.

Habitat and Comments: Although *Phyllymenia gibbesii* is not common in Puerto Rico, it has been collected on rocky substrata in shallow water. [Additional illustrations: as *Grateloupia gibbesii*, Rodriguez-Prieto et al. 2021: fig. 6A–H; Littler et al. 2008: 122.]

Halymeniaceae Bory

Halymenia C.Agardh

Halymenia C.Agardh 1817: xix, nom. cons.

Bladelike thalli are erect, and some species arise from a short stipe. The thallus texture is frequently gelatinous and soft. Blades are simple or branched. The thalli are multiaxial, possessing a filamentous medulla of filaments within a gelatinous matrix. Gangliar cells are generally present within the medulla. Surrounding the medulla is pseudoparenchymatous cortex of dichotomously divided filaments. Spermatangia arise from outer cortical cells. Carpogonial branches are 2-celled and occur in ampullae. Auxiliary cell branches are in separate ampullae. Cystocarps are immersed. Cruciately or decussately divided tetrasporangia are formed in the outer cortex. Seventy-nine species of *Halymenia* are recognized worldwide; three of these occur in Puerto Rico.

KEY TO THE *HALYMENIA* SPECIES OF PUERTO RICO

1. Blade surface with abundant papillae . . . . . *H. duchassaingii*
   Blade surfaces smooth 2
2. Blades pinnately branched . . . . . *H. pseudofloresii*
   Blades entire or lobed . . . . . *H. hancockii*

Halymenia duchassaingii (J.Agardh) Kylin

FIGURE 109
Halymenia duchassaingii (J.Agardh) Kylin 1932: 29.
Basionym: *Meristotheca duchassaingii* J.Agardh 1872: 37.
Puerto Rican Records: As *Halymenia duchassaingii*: Ballantine et al. 2002b.
Western Atlantic Distribution: Cuba, Guadeloupe, Puerto Rico, Brazil, Colombia.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Guadeloupe, French West Indies.

Bladelike thalli reach up to 30 cm in height. The blades branch near the base, giving rise to several oblanceolate segments, 1.0–4.0(–10) cm wide. The margins are irregularly lobed and erose-dentate; the blade surfaces are strongly papillate. Puerto Rican specimens possess colorless medullary cells that measure 8.0–11 µm diam., with local swellings to 35 µm. Large stellate ganglia to 55 µm diam. are common in the medulla. Cruciately divided tetrasporangia are abundantly produced in the cortex and measure to 18 µm in width and to 28 µm in length.

Habitat and Comments: *Halymenia duchassaingii* in Puerto Rico is known only from one collection at Crash Boat Beach, Aguadilla, at 6.0 m depth. [Additional illustrations: Ballantine et al. 2002b: fig. 3; Littler and Littler 2000: 107; Suárez et al. 2015: fig. 85.]

Halymenia hancockii W.R.Taylor

FIGURE 110
Halymenia hancockii W.R.Taylor 1942: 98, pl. 3: fig. 6, pl. 14: figs. 1–5.
Puerto Rican Records: Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a; Ballantine et al. 2016b.
Western Atlantic Distribution: United States (North Carolina, South Carolina, Georgia, Florida), Cuba, Puerto Rico, Colombia.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Near Jalera Point [Galera Point], Colombia.

Thalli with slender, cylindrical stipes, 1.0–3.0 mm long, that bear lanceolate or oblanceolate blades. The blades, to ~10 cm tall, 2.0 cm broad, and 35–40 µm thick, possess obtuse apices and entire margins with rare proliferations. The blades are

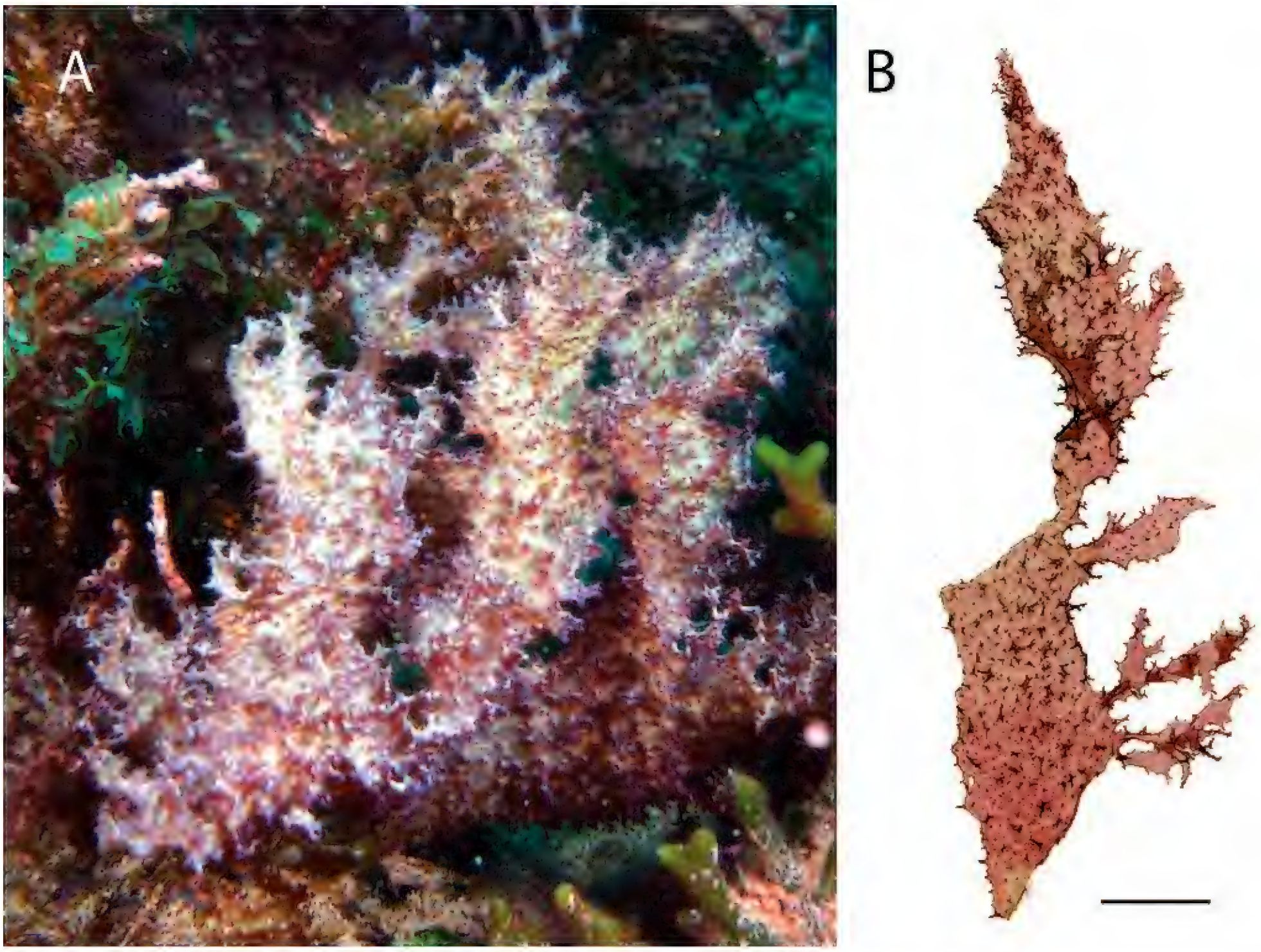

FIGURE 109. *Halymenia duchassaingii*. (A) In situ photograph, Punta Brea, Guánica, 17 m. (B) DLB5523, herbarium specimen, Crash Boat Beach, 2.0 m. Scale bar = 2.0.

generally unbranched but sometimes bifurcate. The medulla is loosely filamentous and lacks stellate ganglia and is surrounded by a 1(–2) layered cortex of 8.0–10 µm diam. cells. Cystocarps measure 200–280 µm diam. Ovoid tetrasporangia, 7.0–13 µm diam. and 12–16 µm long, are scattered between cortical cells. Algae are pinkish to dull reddish purple in color.

Habitat and Comments: *Halymenia hancockii*, known to depths of 55 m in Puerto Rico, has been found exclusively epizoically on *Strombus pugilis* L. on muddy bottoms. [Additional illustrations: Schneider and Searles 1991: figs. 332, 333.]

Halymenia pseudofloresii Collins et M.Howe

FIGURE 111

Halymenia pseudofloresii Collins et M.Howe 1916: 177.

Misapplied Name: Halymenia floresii sensu Taylor 1960: 418 [non *Halymenia floresii* (Clemente) C.Agardh 1817: xix, as "*floresia*"].

Puerto Rican Records: As *Halymenia pseudofloresii:* Ballantine and Wynne 1986; Ballantine et al. 2016b. As *Halymenia floresii*: Almodóvar and Blomquist 1961; Almodóvar 1964a, 1964b, 1965; Díaz-Piferrer and Caballer de Pérez 1964; Ballantine 1979, 1984; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a.

Western Atlantic Distribution: Belize, Caribbean Mexico, Bermuda, Barbados, Cuba, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Barthélemy, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Walsingham grotto, Walsingham Park, Bermuda.

Thalli are foliaceous, with gelatinous membranous blades. Stipes are 5.0–10 mm long, supporting obovate, frequently elongate blades, 7.0–40 cm in length, 1.0–20(–35) cm wide, and 120–400 µm thick. The blades are pinnately divided or are irregularly subpalmately lobed, frequently with marginal

FIGURE 110. *Halymenia hancockii*. DLBsn, herbarium specimen, leeward Laurel Reef, living on *Strombus pugilis*, 18 m. Scale bar = 1.0 cm.

linear proliferations. The medulla is loosely filamentous, with filaments 3.0–16 µm diam. Stellate ganglia, 20–40 µm diam., are not common. The cortex is 2–6 cells thick. Inner cortical cells measure 10–55 µm diam., and the peripheral cortical cells are elongated longitudinally and measure 4.0–10 µm diam. Gametophytes are dioecious. Spherical cystocarps, 70–180 µm diam., do not project from the surface. Carposporangia measure 5.0–22 µm diam. Ovoid tetrasporangia measure 10–18 µm diam. and 13–30 µm long. Algae are pink to deep red in color.

Habitat and Comments: Collected at intermediate depths in Puerto Rico, to 60 m, *Halymenia pseudofloresii* is a common element at the algal plains offshore from the southern coast of Puerto Rico. Schneider et al. (2010) found that Bermudan species attributable to *H. floresii* belonged to *H pseudofloresii* and questioned the existence of *H. floresii* in the western Atlantic. [Additional illustrations: as *Halymenia floresii*: Littler et al. 2008: 124; Braune and Guiry 2011: fig. 184.1.]

Nemastomatales Kylin

Schizymeniaceae Masuda et Guiry

Platoma Schousb. ex F.Schmitz

Platoma Schousb. ex F. Schmitz 1894: 627.

Gametophyte thalli of erect, broad unbranched or variously branched blades are uncalcified and mucilaginous and compressed or flattened. Thalli are structurally multiaxial, with a medulla of loose filaments and a cortex of dichotomously divided filaments. Vesicular cells are generally present in the inner cortex. Subsidiary auxiliary cells are formed from cells of

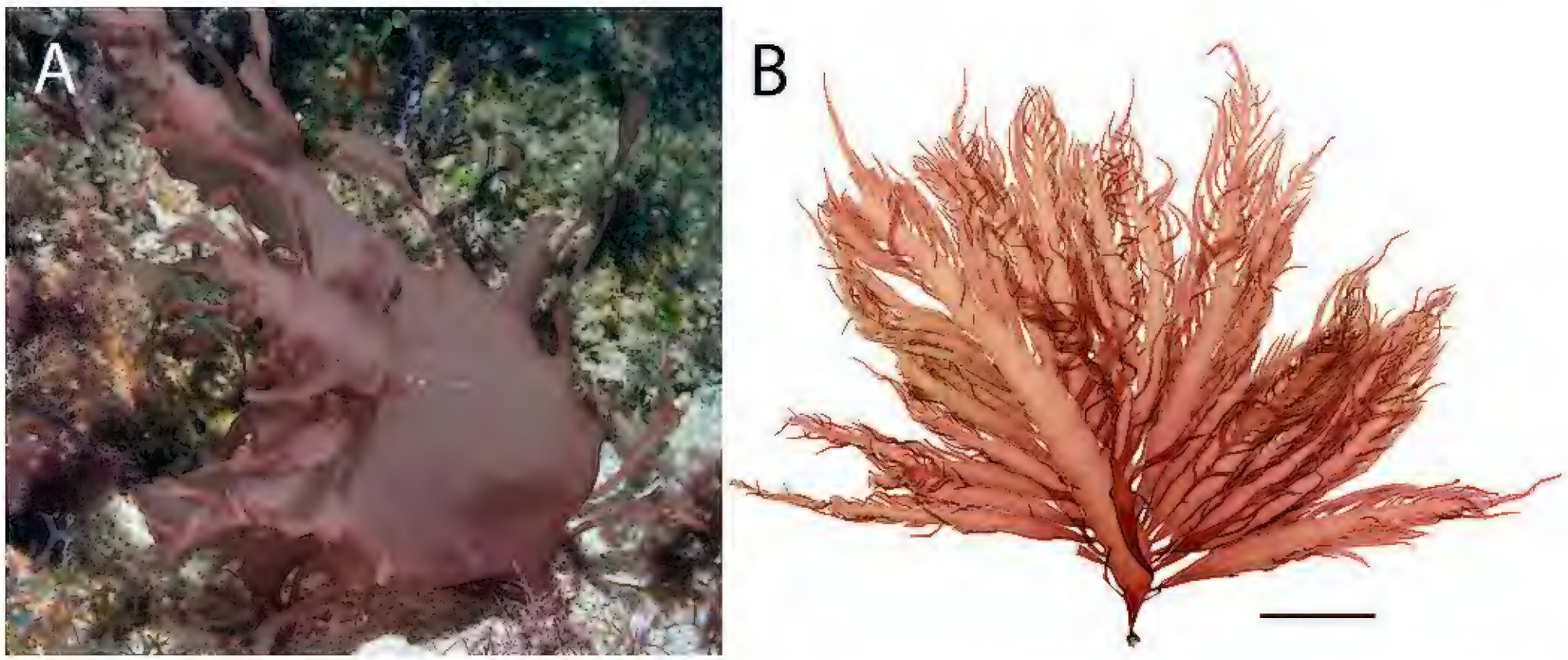

FIGURE 111. *Halymenia pseudofloresii*. (A) In situ photograph, 1.5 km seaward Media Luna Reef, 17 m. (B) DLB1597, herbarium specimen, algal plain, 1.5 km seaward Media Luna Reef, 17 m. Scale bar = 2.0 cm.

the cortical fascicle adjacent to the supporting cell. Connecting filaments formed from subsidiary auxiliary cells course through the thallus to intercalary generative auxiliary cells. Gonimoblasts arising from a diploidized generative auxiliary cell are composed entirely of carposporangia. There are 11 recognized *Platoma* species, 1 of which is known to Puerto Rico.

KEY TO THE *PLATOMA* AND *PREDAEA* SPECIES OF PUERTO RICO

1. Thalli nearly spherical, to 14 mm in height ..... ***Pr. goffiana***
   Thalli not spherical, taller than 14 mm. 2
2. Thalli strongly compressed to flat with abundant marginal branchlets ..... ***Pl. gelatinosum***
   Thalli not as above 3
3. Thalli compressed; spherical to ovoid outer cortical cells; gland cells present ..... ***Pr. laciniosa***
   Thalli subcylindrical; linear to oblong outer cortical cells; gland cells absent 4
4. Gonimoblast origin is terminal on auxiliary cells; nutritive cells few ..... ***Pr. weldii***
   Gonimoblast origin from auxiliary cells is lateral; nutritive cells many ..... ***Pr. feldmannii***

Platoma gelatinosum (M.Howe) C.W.Schneid., McDevit, G.W.Saunders et C.E.Lane

FIGURE 112

Platoma gelatinosum (M.Howe) C.W.Schneid., McDevit, G.W.Saunders et C.E.Lane 2011: 323, figs. 1–10.

Basionym: *Nemastoma gelatinosum* M.Howe 1918a: 536.

Heterotypic Synonym: *Platoma chrysymenioides* Gavio, Hickerson et Fredericq 2005: 45, figs. 3–24.

Misapplied Name: Platoma cyclocolpum sensu Taylor 1960: 437, pl. 43: fig. 4 [non *Platoma cyclocolpum* (Montagne) F.Schmitz 1894: 627].

Puerto Rican Records: The species is newly reported from Puerto Rico herein. DLB8307, Coll. HR, 1.iv.2011, west of lighthouse at Rincón, Puerto Rico, 28 m depth (US Alg. Coll. 222378); DLB8324, Coll. HR, 9.iv.2011, west of lighthouse at Rincón, Puerto Rico, 28 m depth (US Alg. Coll. 222379).

Western Atlantic Distribution: Caribbean Mexico, United States (Florida, Louisiana), Bermuda, Guadeloupe, Martinique, Puerto Rico, Netherlands Antilles.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Castle Harbor near Tucker's Town, Bermuda.

Algae are lubricous and compressed to flat, reaching up to 20 cm in height with irregular marginal lobes that are abundantly beset with acute proliferations. Branching is mostly in a single plane. Thalli arise from a short expanding stipe. Thalli are multiaxial with hyaline medullary filaments, 3.0–4.0 µm diam., that produce a cortex of pseudodichotomously divided fascicles. The cortical cells are moniliform, measuring 3.0–15 µm long and 1.7–6.0 µm diam. Innermost cortical cells are subcylindrical, and distal cortical cells are ovoid in shape. Gland cells, averaging 25 µm diam., are abundantly produced. Reproductively, the species apparently possesses an alternation of heteromorphic generations. Carpogonial branches are 3-celled and borne distally on a supporting cell at the base of a pseudodichotomy. Spermatangia are borne terminally on cortical cells, either singly or in pairs. Algae are purplish to red in color.

Habitat and Comments: *Platoma gelatinosum* grows on rocks from the intertidal to 20 m depth. Puerto Rican thalli measure to approximately 15 cm in height and were nonreproductive. Schneider et al. (2011) reported two seasonal morphological entities from Bermuda, a small flattened and marginally proliferous alga collected in the winter that was reported as *Platoma cyclocolpum* and a large irregularly branched alga collected in the summer and reported as *Nemastoma gelatinosum*. On the basis of a multigene molecular analysis, the latter was transferred to *Platoma*, and the former was placed in synonymy with it. Schneider et al. (2011) also placed *Platoma chrysymenioides* in synonymy with *P. gelatinosum*. The Puerto Rican specimens conform to the larger summer thallus morphology. [Additional illustrations: as *Platoma cyclocolpum*, Gabriel et al. 2010: figs. 1–34; as *Platoma chrysymenioides*, Gabriel et al. 2010: figs. 37–40.]

Predaea G.De Toni

Predaea G.De Toni, 1936: [5].

Gelatinous thalli are globose, peltate, terete, or bladelike, with soft, gelatinous blades either inflated or compressed. Structurally, thalli are composed of loose medullary filaments and rhizoids surrounded by a cortex of pigmented, branched filaments that sometimes possess intercalary gland cells. The cortical cells are generally ellipsoidal. Life histories involve a heteromorphic alternation of generations. Gametophytes are monoecious or dioecious. Spermatangia occur as clusters on outer cortical cells. Carpogonial branches are 2- or 3-celled and are cut off from inner cortical supporting cells. Auxiliary cells possess clusters of nutritive cells ("cellules") attached to immediately adjacent cortical cells. Gonimoblast initials arise laterally from the connecting filament at the point of fusion to an auxiliary cell. Cruciately divided tetrasporangia are borne on a reduced filamentous tetrasporophyte phase, consisting of small, *Audouinella*-like thalli. Four of the 21 recognized *Predaea* species are found in Puerto Rico.

Predaea feldmannii Børgesen

FIGURE 113

Predaea feldmannii Børgesen 1950: 7, figs. 1–3.

Puerto Rican Records: Ballantine and Wynne 1986; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina, Georgia), Martinique, Puerto Rico, Brazil, Colombia, Venezuela.

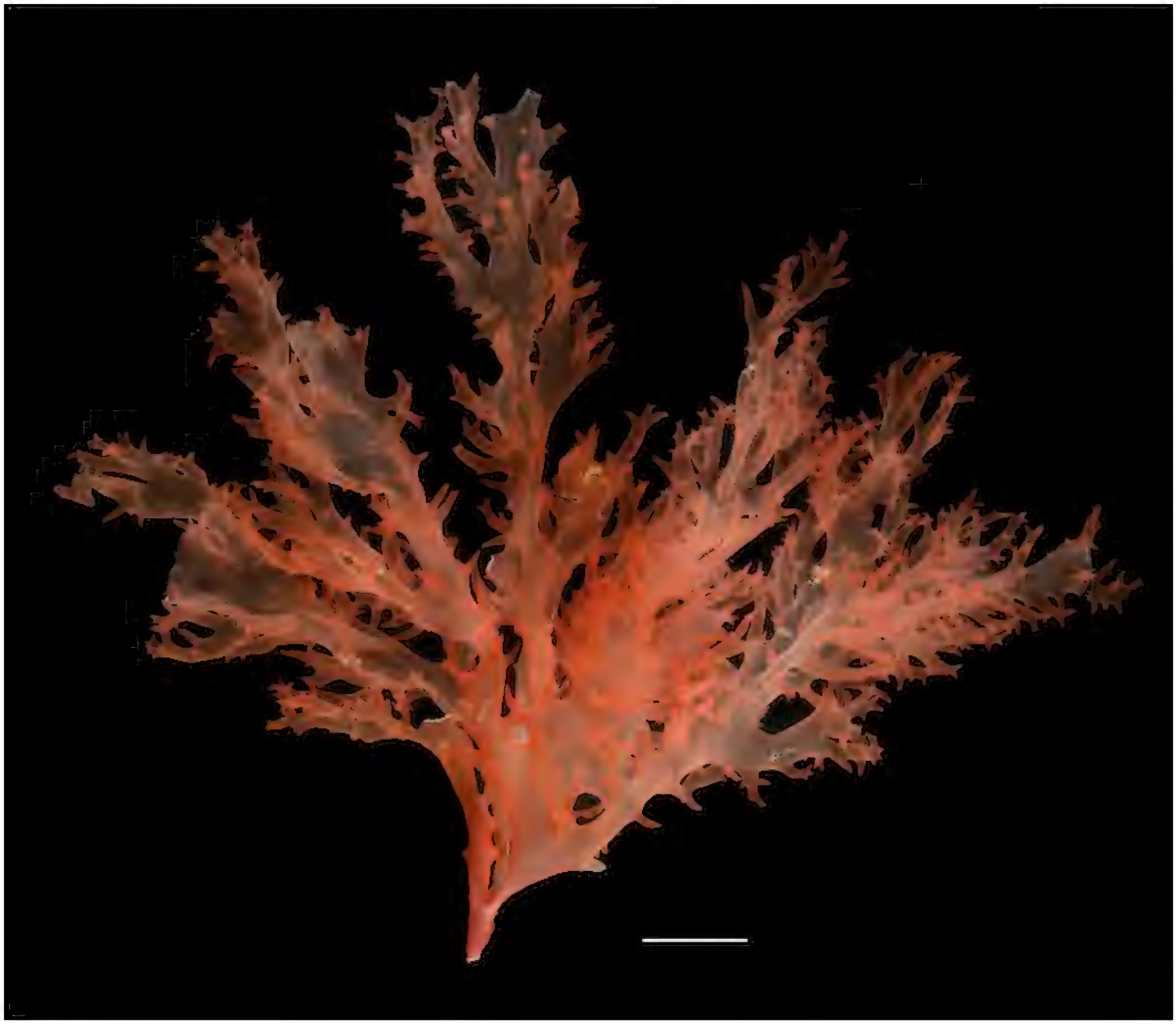

FIGURE 112. *Platoma gelatinosum*. Live specimen, Rincon, 28 m. Scale bar = 2.0 cm.

World Distribution: See Guiry and Guiry 2024.
Type Locality: Prosperous Bay, St. Helena.

Thalli, reaching up to 14 cm in height, form subcylindrical to flattened or compressed blades that are irregularly divided along the margins. Axes, to 0.5–6.0 cm wide and to 1.0 cm thick, possess surface papillae. The medulla possesses both thin, ~4.0 µm diam., and thicker, ~7.0–8.0 µm diam., filaments. The cortex is composed of repeatedly branched assimilatory filaments, ~300 µm long, whose cells are oval, to 10 µm diam. and 30–40 µm long. Gametophytes are dioecious. Spermatangia are produced on distal cortical cells. The carpogonial branch is variously reported as 2 or 3-celled, and the mature auxiliary cell is nearly spherical or broadly oval, 25–30 µm broad and 30–35 µm long. Nutritive cell clusters occur in branched chains of 5–6 cells. Gonimoblasts are pyriform, 110 µm diam. and 220 µm long. Algae are rose red in color.

Habitat and Comments: *Predaea feldmannii* has rarely been collected in Puerto Rico; most of the collections are from the offshore algal plains on the southern Puerto Rican coast. [Additional illustrations: Kraft and John 1976: figs. 11–30; Guimarães and Amado-Filho 2008: figs. 27–29.]

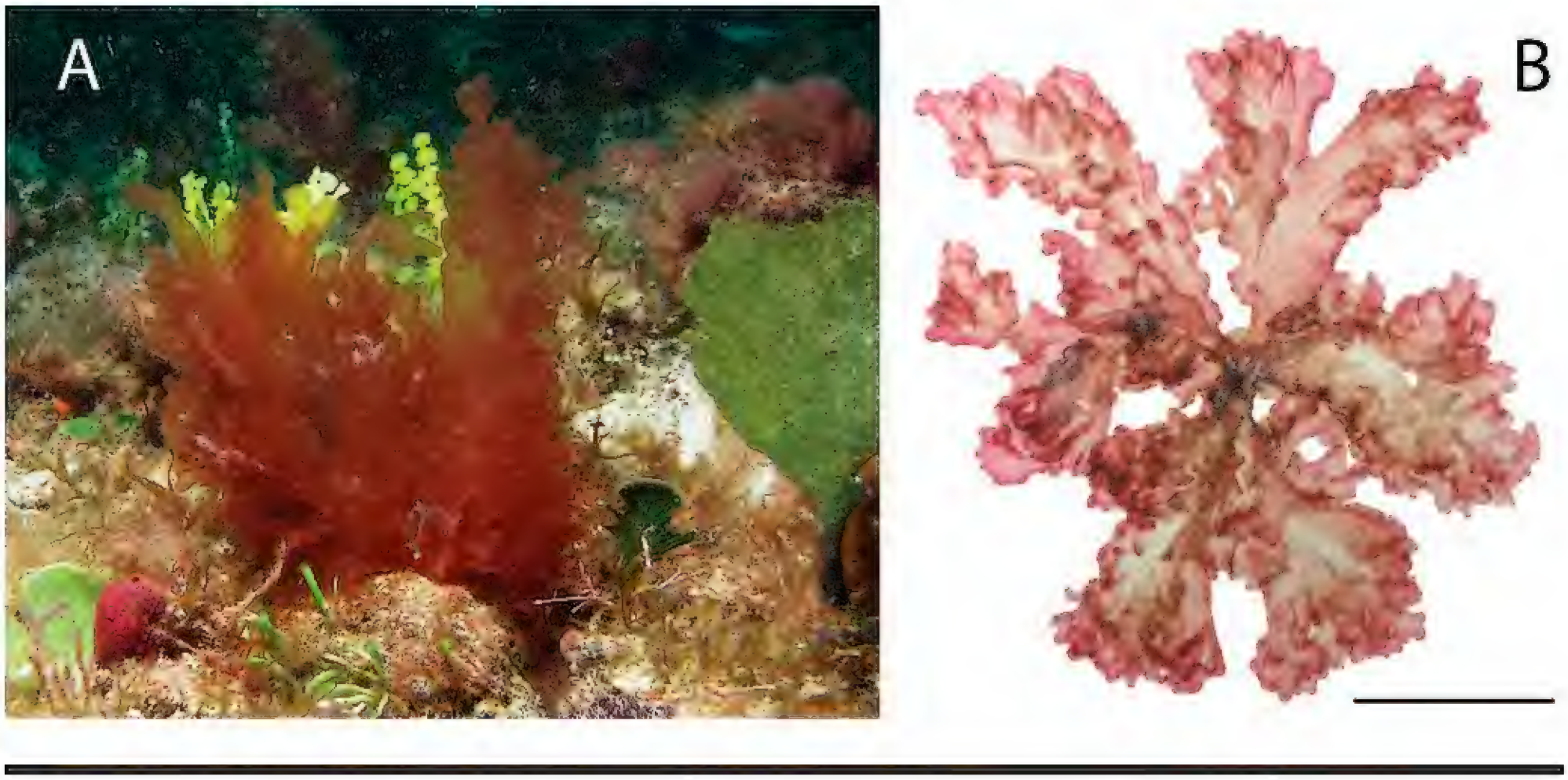

FIGURE 113. *Predaea feldmannii*. (A) In situ photograph, 1.5 km seaward Media Luna Reef, 17 m. Field is approximately 20 cm. (B) DLB5578, herbarium specimen, algal plain, 1.5 km seaward Media Luna Reef, 17 m. Scale bar = 5.0 cm.

Predaea goffiana D.L.Ballant., H.Ruiz et N.Aponte

FIGURE 114

Predaea goffiana D.L.Ballant., H.Ruiz et N.Aponte 2002a: 385, figs. 10–11.

Puerto Rican Records: Ballantine and Aponte 2002a; Ballantine et al. 2002b.

Western Atlantic Distribution: Bermuda, Caribbean Mexico, Puerto Rico.

World Distribution: See Guiry and Guiry 2024.

Type Locality: 1 km seaward Laurel Reef, La Parguera, Puerto Rico.

Thalli, to 14 mm in height, are composed of compressed lobes, measuring 2.0 mm in thickness, that enlarge to an irregularly rounded shape. Lobes lack marginal undulations or surface protuberances. Structurally, algae possess medullary cells, 3.0–4.0 µm diam., that give rise to branched cortical fascicles that branch dichotomously, unilaterally, alternately, or, rarely, oppositely. The cortical cells, 3.0 µm in diam., are cylindrical in shape and frequently Y-shaped immediately proximal to a dichotomy. Gland cells are not produced. Gametophytes are monoecious. Spermatangia are cut off from short, whorled spermatangial mother cells that are cut off from the distal 2 or 3 cells of cortical filaments. Carpogonial branches are 3 cells in length. Auxiliary cells are inconspicuous due to their only slightly enlarged diameters. Cells contiguous to the auxiliary cells each produce 1 or, rarely, 2 nutritive cells. Obovate or irregularly spherical carposporophytes, to 110 µm diam., possess 2 or 3 gonimolobes. Algae are pink to bright red in color.

Habitat and Comments: *Predaea goffiana* is uncommon in Puerto Rico, with specimens collected subtidally from depths of 9 to 15 m on coral fragments as well as epizoically on the tunicate *Polycarpa spongiabilis* Traustedt.

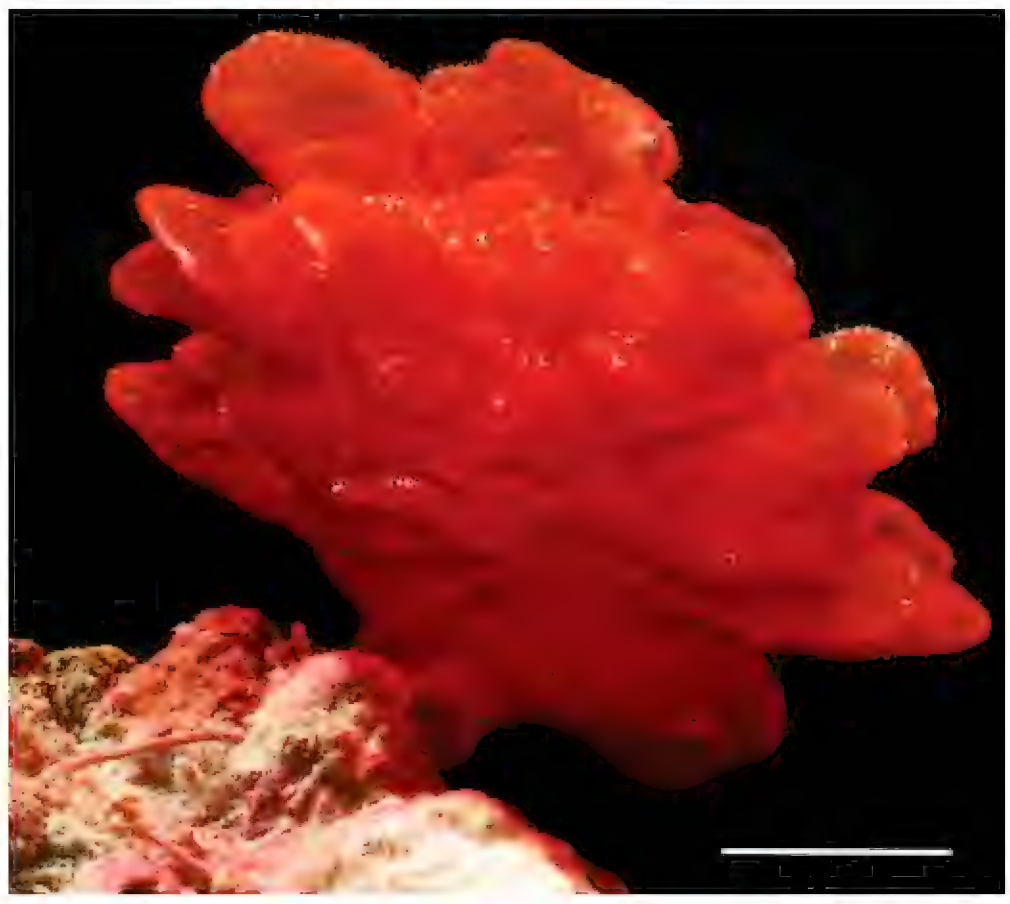

FIGURE 114. *Predaea goffiana*. Habit of live specimen, Laurel Reef, 15 m. Scale bar = 5.0 mm.

Predaea laciniosa Kraft

FIGURE 115

Predaea laciniosa Kraft 1984: 11, figs. 25–35.
Puerto Rican Records: Ballantine et al. 2009, 2016b.
Western Atlantic Distribution: Puerto Rico, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Heron Island, Great Barrier Reef, Australia.

Thalli are irregularly lobed in more than one plane, to 1.0 cm thick and reaching 2.0–5.0 cm in height. Thalli are gelatinous in texture, and lobe apices are obtuse. The medulla consists of loosely arranged filaments, 2.0–3.0 µm diam., within a mucilaginous gel. Cortical filaments are dichotomously branched, composed of ovoid cells, 4.0–5.0 µm diam., that rarely bear spherical, intercalary gland cells, 13–26 µm diam. Spherical spermatangia, 2.0–3.0 µm diam., are borne on apical or subapical cortical cells. Carpogonial branches are 3-celled. Ovoid cystocarps, 78–126 µm diam., possess ovoid to spherical carposporangia, 4.0–8.0 µm diam. Algae are pink to rose red in color.

Habitat and Comments: In Puerto Rico, *Predaea laciniosa* is known from deep water, 61 and 63 m depths at the edge of the southern insular shelf. *Predaea laciniosa* has a limited distribution in western Atlantic Ocean localities. Both *Predaea masonii* (Setchell and N. L. Gardner) and *P. weldii* also have Atlantic and Pacific distributions (Kajimura 1987; Guiry and Guiry 2024).

FIGURE 115. *Predaea laciniosa*. DLB7520, habit of live specimen, edge of insular shelf offshore from La Parguera, 62 m. Scale bar = 1.0 cm.

Predaea weldii Kraft et I.A.Abbott

FIGURE 116

Predaea weldii Kraft et I.A.Abbott 1971: 194, figs. 1–15.
Puerto Rican Records: Ballantine and Aponte 1997a, 1997b, 2002a.
Western Atlantic Distribution: Puerto Rico, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Kaneohe Bay, Oahu, Hawaii.

Erect, gelatinous thalli, 5.0–8.0 mm thick, reach 10–15 cm in height. Immature blades are expanded, lobed, and bullate, becoming compressed or terete and lobed. The medulla is composed of slender, little-branched filaments within a gelatinous matrix. The cortex is composed of dichotomously branched filaments. The cortical cells are moniliform in immature thalli, becoming rectangular. Gland cells occur on subcortical cells. Gametophytes are monoecious. Spermatangial clusters are located on terminal cortical cells. Carpogonial branches are 3-celled, cut off by inner cortical cells. Auxiliary cells are intercalary within cortical filaments. Spherical nutritive cells, up to 8, are cut off by the cortical cells immediately proximal to and 2 cells distal to the auxiliary cell. The primary gonimoblast initial develops from the auxiliary cell apex and is directed outward. Tetrasporangia are unknown. Algae are deep pink to dark red in color.

Habitat and Comments: In Puerto Rico, *Predaea weldii* has been collected seaward of Isla San Cristobal, La Parguera, at 17 m depth.

Schizymeniaceae Masuda et Guiry

Titanophora (J.Agardh) Feldmann

Titanophora (J.Agardh) Feldmann 1942: 111.

Gametophyte thalli are erect or decumbent. Thalli are attached by discoid holdfasts in addition to secondary attachments. The axes are bladelike or foliaceous and slightly mucilaginous in texture. Branching is irregularly lateral or dichotomous. Algae are structurally multiaxial with a loose filamentous medulla and a cortex of anticlinally branched filaments. Ovoid to elongate intercalary vesicular cells are usually present in the inner cortex. Light calcification is restricted to the medulla. Gametophytes are monoecious. Spermatangia are cut off by outer cortical cells. Carpogonial branches are 2 or 3-celled and are borne on inner cortical cells. Cystocarps are immersed and surrounded by lax involucral filaments; tetrasporophytes are unknown. One of the eight recognized *Titanophora* species occurs in Puerto Rico.

Titanophora incrustans (J.Agardh) Børgesen

Titanophora incrustans (J.Agardh) Børgesen 1949: 4, pl. 1.
Basionym: *Halymenia incrustans* J.Agardh 1885:15.

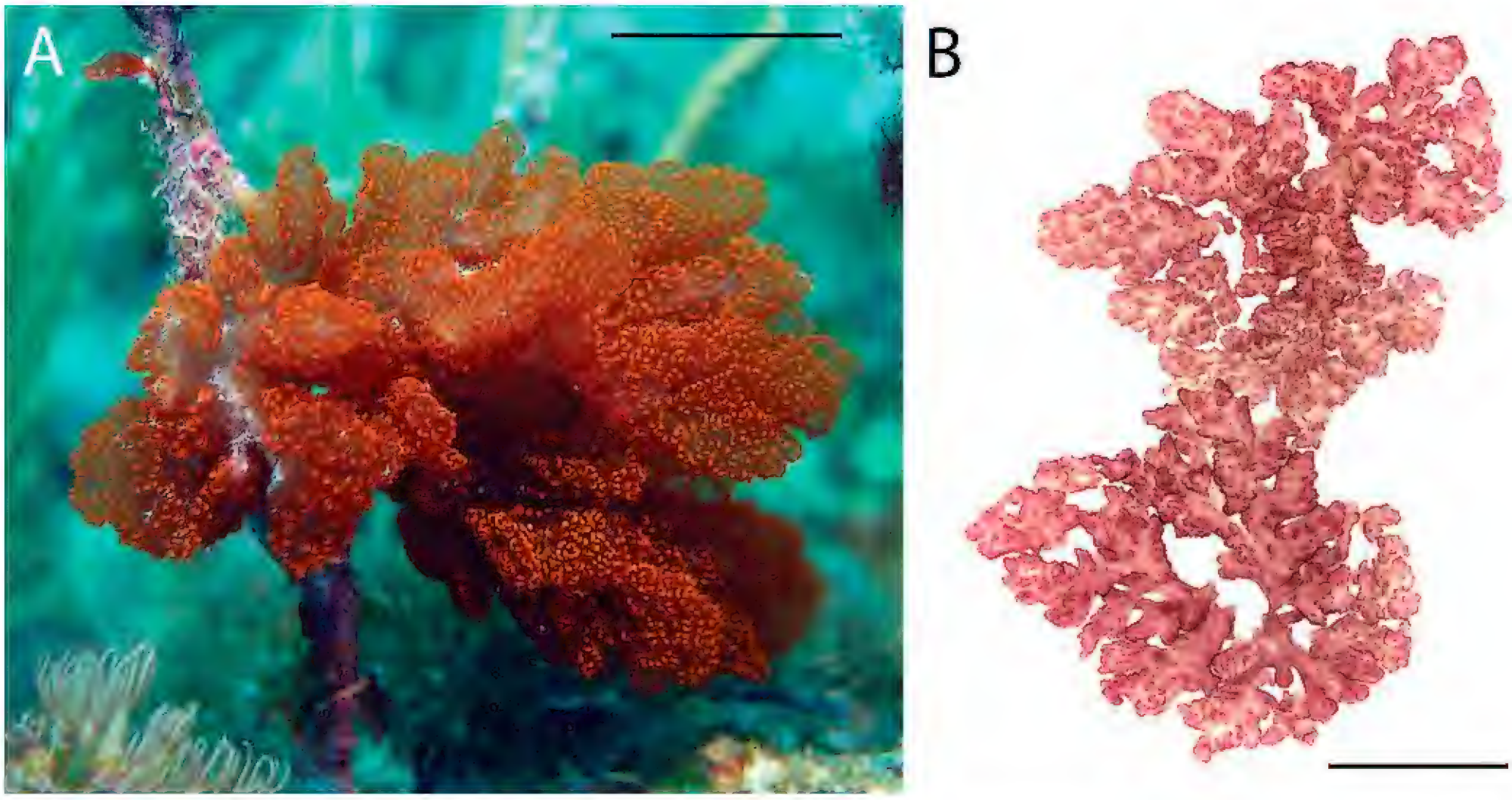

FIGURE 116. *Predaea weldii*. (A) In situ photograph, 1.5 km seaward Media Luna Reef, 17 m. Field is approximately 7.0 cm. (B) DLB5579, herbarium specimen, 1.5 km seaward Media Luna Reef, 17 m. Scale bar = 5.0 cm.

Puerto Rican Records: As *Titanophora incrustans*: Ballantine and Aponte 1997b, 2002a; Ballantine et al. 2016b.
Western Atlantic Distribution: Caribbean Mexico, United States (Florida), Grenadines, Puerto Rico, Colombia.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Florida, USA.

Thalli are foliaceous and lightly calcified, reaching to ~14 cm in height. Primary axes are subsimple, 4.0–20 mm wide and 0.5–1.3 mm thick, and marginally pinnately branched. Medullary filament cells are 15–30 µm diam. and 200–400 µm long. The filaments are frequently branched. Gland cells are spherical or oval, 30–40 µm diam. and 35–70 µm long, or irregularly shaped. Ultimate cortical cells are spherical, 8.0–12 µm diam., or elongate, to 10 5.6–14 µm diam. long. The life history involves an alternation of isomorphic generations. Algae are dull white to pinkish in color; when dried, the surface appears roughened.

Habitat and Comments: Only a single small, to 4.0 cm tall, specimen has been collected in Puerto Rico. The sterile specimen was dredged offshore from Punta Agujereada, Aguadilla at a depth of 60 m. Bucher and Norris (1992) noted that characters utilized for discrimination among *Titanophora* species are not reliable and speculated that there may be a single variable species comprising the genus. [Illustrations: Ballantine and Aponte 1997b: fig. 4; Littler and Littler 2000: 93.]

Peyssonneliales Krayesky, Fredericq et J.N.Norris

Peyssonneliaceae Denizot

Agissea Pestana, Lyra, Cassano et J.M.C.Nunes

Agissea Pestana, Lyra, Cassano et J.M.C.Nunes 2021 in Pestana et al. 2021: 1755.

Thalli are completely or partially adhered to the substratum with hypobasal calcification and by unicellular rhizoids. Hypothallial filaments are in either a parallel or flabellate arrangement. Tetrasporangia are cruciately divided, forming at the ends of the perithallial filaments.

Comments: The genus is essentially not vegetatively differentiated from *Peyssonnelia*; however, it differs molecularly. Twelve species of *Agissea* are recognized; one of these is known from Puerto Rico. *Agissea* is included in "Key to the *Agissea* and *Peyssonnelia* Species of Puerto Rico" below under the genus *Peyssonnelia*.

Agissea inamoena (Pilg.) Pestana, Lyra, Cassano et J.M.C.Nunes

FIGURE 117

Agissea inamoena (Pilg.) Pestana, Lyra, Cassano et J.M.C.Nunes in Pestana et al. 2021: 1757.

Basionym: Peyssonnelia inamoena Pilg. 1911: 311, figs. 24, 25.

Misapplied Name: *Peyssonnelia rubra* sensu Taylor 1960: 371 [non *Peyssonnelia rubra* (Grev.) J.Agardh 1851: 502].

Puerto Rican Records: As *Peyssonnelia inamoena*: Ballantine et al. 2016b. As *Peyssonnelia rubra*: Hauck 1888; Almodóvar and Blomquist 1959; Taylor 1960; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002a.

Western Atlantic Distribution: Caribbean Mexico, United States (North Carolina, South Carolina, Florida), Bahamas, Cuba, Puerto Rico, Brazil.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Gross, Batanga, Cameroon, West Africa.

Thalli are crustose, with blades 2.0–5.0 cm broad and to 215 µm thick in vegetative portions, and possess radial and concentric lines. The crusts, with unicellular rhizoids, are loosely attached. Calcification is hypobasal. Hypothallial filaments, in staggered parallel rows, are composed of cells, 7.0–15 µm diam., 18–38 µm long, and to 26 µm high. Coxal cells are boot shaped and give rise to 2 ascending perithallial filaments. The perithallial filaments are 3–6 cells in length. Gametophytes are presumably dioecious. Spermatangia are cut off in linear chains. Carpogonial and auxiliary cell branches are 4–6-celled. Globose to compressed carposporangia, to 105 µm diam., are cut off in chains of 2–4. Cruciately divided tetrasporangia, 27–57 µm diam. and 70–100 µm long, occur in elevated nemathecia. Algae are pink to rosy red in color.

Habitat and Comments: *Agissea inamoena* is probably the most common shallow-water Peyssonneliaceae species in Puerto Rico and has also been reported to 73 m depth (Ballantine et al. 2016b). Schneider and Reading (1987) concluded that algae referred to *Peyssonnelia rubra* from the southeast United States and the Bahamas were *P. inamoena* Pilg. They recommended that Caribbean material be critically compared to *P. inamoena* as well. On the basis of a large-scale molecular analysis, Pestana et al. (2021) segregated *Agissea* from *Peyssonnelia*. Their sequences, however, did not include specimens from the type locality. [Additional illustrations: as *Peyssonnelia inamoena*, Cordeiro-Marino 1978: figs. 83–88; Schneider and Searles 1991: figs. 298–301; Guimarães and Fujii 1999: figs. 52–65.]

FIGURE 117. *Agissea inamoena*. DLB8493, live specimen, Magueyes Island, 0.5 m. Scale bar = 1.0 cm.

Metapeyssonnelia Boudour., Coppejans et Marcot-Coq.

Metapeyssonnelia Boudour., Coppejans et Marcot-Coq. 1976: 288.

Thalli are orbicular, attached to the substratum by unicellular rhizoids. Calcification is hypobasal or complete. Structurally, thalli are polymorphic with a "*Peyssonnelia*-type" morphology in which thalli produce a single-layered hypothallus that gives rise to dorsally directed files of cells. This arrangement becomes disrupted locally to a fountain-like arrangement in which the hypothallus gives rise to upwardly (superior) and downwardly (inferior) directed filaments or a perithallial filament initiates a branch that acts as a hypothallial filament of cells or a perithallial filament continues to branch laterally. Gametophytes are unknown. Tetrasporangia occur in nemathecia. The addition of a new species herein raises the total number of the species known in the genus to six. Four species of *Metapeyssonnelia* are now recognized in Puerto Rico.

KEY TO THE *METAPEYSSONNELIA* SPECIES OF PUERTO RICO

1. Crusts are up to 950 µm in thickness, lacking cystoliths 2
   Crusts are less than 650 µm in thickness, cystoliths present 3
2. Thalli bright orange when living, crusts to 950 µm in thickness . . . . . ***M. tangerina***
   Thalli multicolored, red and orange; crusts variable in thickness, 320 to 830 µm in thickness . . . . . ***M. mesophotica***
3. Thalli are deep purple, appearing nearly black when living; tetrasporangial nemathecia superficial . . . . . ***M. corallepida***
   Thalli mottled reddish brown when living; tetrasporangial nemathecia immersed . . . . . ***M. milleporoides***

Metapeyssonnelia corallepida M.Verlaque, Ballest. et Antonius

FIGURE 118

Metapeyssonnelia corallepida M.Verlaque, Ballest. et Antonius 2000: 191–192, figs. 2–27.

Puerto Rican Records: Ballantine et al. 2004; Reyes-Conteras et al. 2016.

Western Atlantic Distribution: Belize, North America, Puerto Rico.

Type Locality: John Pennekamp Coral Reef State Park, off key Largo, Florida, USA.

Crustose thalli spread up to 10–15 cm in extent and are 300–650 µm thick. The crusts are orbicular in shape and completely adherent to the substratum. Hypothallus cells, 11–32 µm diam., are arranged in a fanlike organization and produce short unicellular rhizoids, 18–36 µm diam. Perithallial filaments, measuring 18–55 µm diam. proximally and decreasing to 10–22 µm diam. distally, are cut off singly from hypothallus cells. Cystoliths may be present in the lower thallus. Hairs are borne terminally on widened perithallial filament cells. Tetrasporangial nemathecia, 90–150 µm thick, are borne on the dorsal crust surface. Paraphyses, 2.5–6.5 µm diam., are simple to branched. Tetrasporangia, 40–69 µm diam. and 100–150 µm long, are cut off laterally from proximal cells of fertile paraphyses. Algae are dark purple to nearly black in color.

Habitat and Comments: *Metapeyssonnelia corallepida* was initially found overgrowing the hydrocorals *Millepora complanata* Lamarck and *Millepora alcicornis* L. as well as other corals. At the time of its initial discovery, *M. corallepida* was reported to begin colonization at the dead base of coral colonies and then proceed upward, resulting in overgrowth of the live coral, killing its host (Antonius and Ballesteros 1998). In Puerto Rico, extensive carpets covering living *Millepora complanata* (Lam.) and on coral rubble are observed in shallow back-reef environments in La Parguera. Presumably by release of extracellular allelopathic metabolites, coral tissue is bleached ahead of the encroaching crusts of both *Metapeyssonnelia corallepida* and *M. milleporoides*. Application of crude lipophilic extracts of both *Metapeyssonnelia* species elicits a bleaching response similar to *Millepora complanata* Lamarck (Reyes-Conteras et al. 2016).

Metapeyssonnelia mesophotica D.L.Ballant. et H.Ruiz sp. nov.

FIGURE 119

Metapeyssonnelia mesophotica D.L.Ballant. et H.Ruiz sp. nov.

Holotype: DLB7942 (US Alg. Coll. 238342), edge of insular shelf ("Hole in the Wall"), 67 m, Coll. HR, 18.11.2009.

Paratypes: DLB7479 (US Alg. Coll. 238355), edge of insular shelf ("Hole in the Wall"), Coll. HR, 63 m, 15.v.2008; DLB7821 (US Alg. Coll. 238354), DLB7522 (US Alg. Coll. 238343), "Barranca," edge of insular shelf off La Parguera, Coll. HR, 57 m, 10.vi.2008; DLB7800 (US Alg. Coll. 238342), edge of insular shelf ("Black Wall"), Coll. HR, 49 m, 5.v.2009.

Etymology: The species epithet is in reference to the exclusively deepwater habitats where the alga lives.

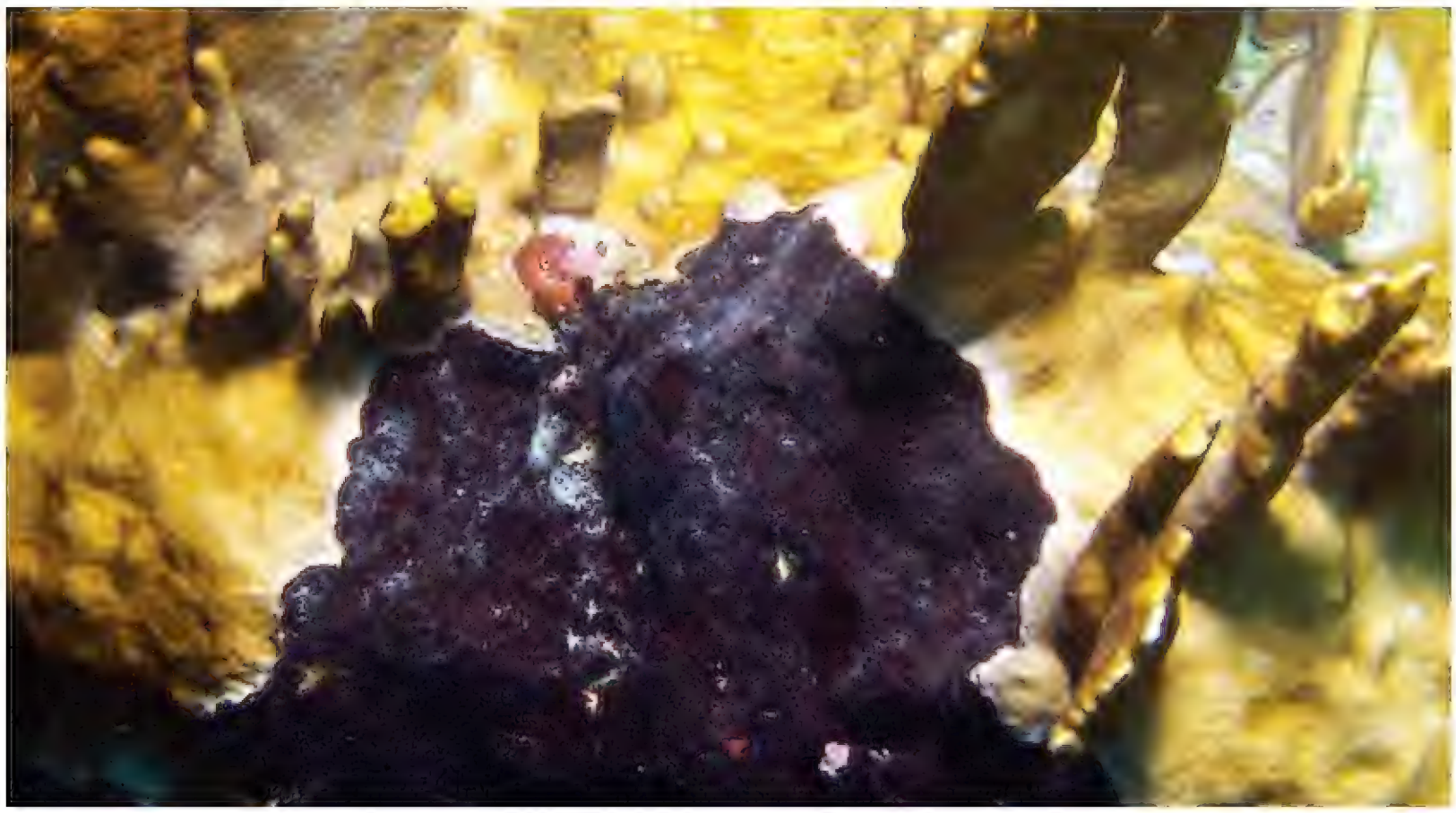

FIGURE 118. *Metapeyssonnelia corallepida*. In situ photograph, San Cristobal Reef, growing on *Millepora complanata* Lamark, 1.0 m. Field is approximately 20 cm.

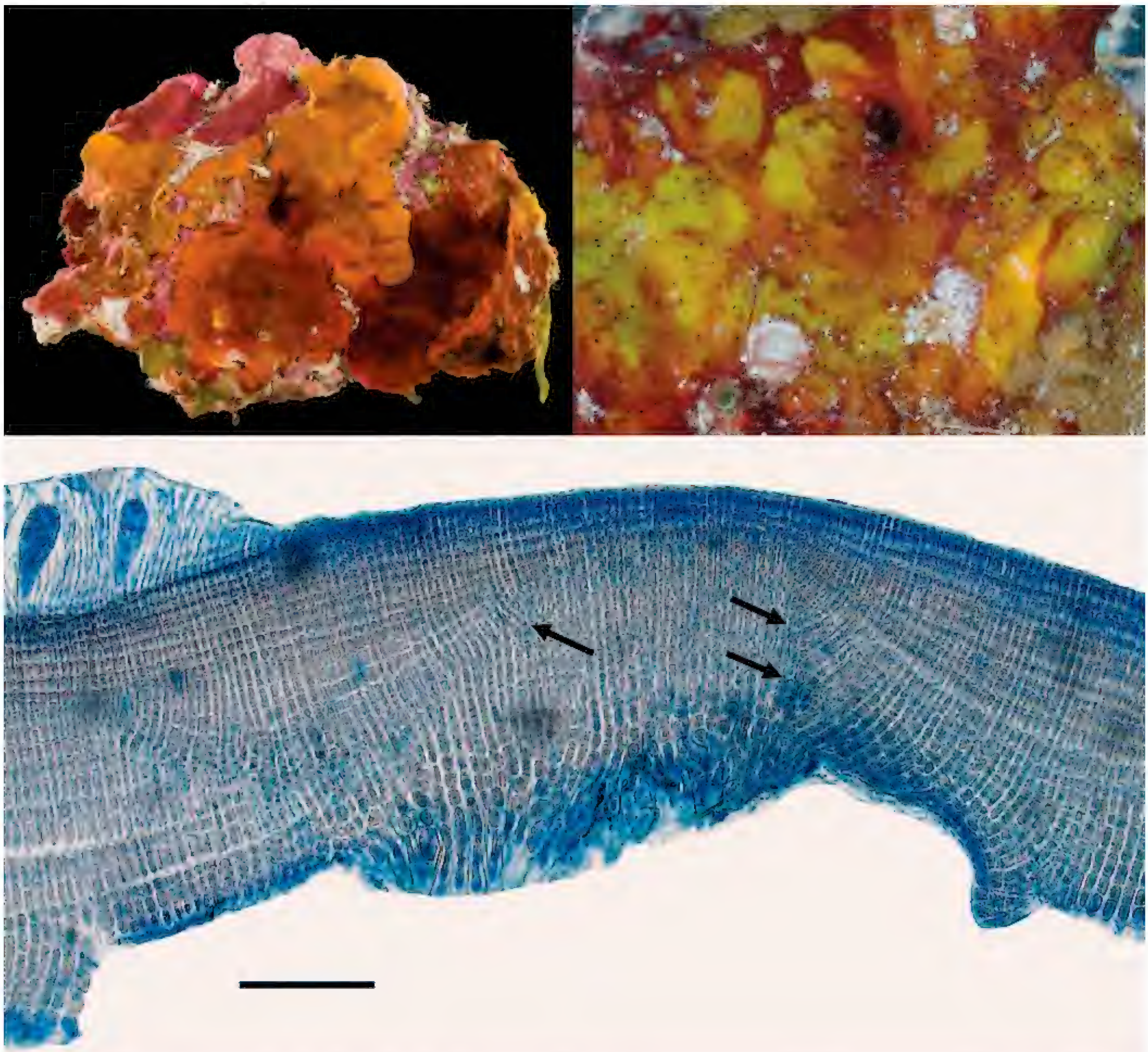

FIGURE 119. *Metapeyssonnelia mesophotica*. (Top left) DLB7522, live specimen of holotype, edge of insular shelf off La Parguera, 57 m. Field = 8.0 cm. (Top right) Close-up of thallus surface, showing imbricating blades. Field = 2.0 cm. (Bottom) DLB7522, longitudinal transverse section. Arrows indicate lateral branching from ascending perithallial cells. Scale bar = 100 µm.

Thalli form extensive crusts to greater than 80 cm in extent, lacking radial lines. Crust surfaces are smooth and noncalcified and possess occasional wartlike excrescences. Crusts possess hypobasal calcification and are closely adherent to the substratum. Thalli are attached by short, to 12 µm long, or nearly spherical rhizoids. Hypothallial cells occur in fan-shaped arrangements. The hypothallus cells measure 23–28 µm long and to 20 µm high when viewed in radial transverse section. Coxal cells are roughly spherical and measure 15–18 µm diam. Perithallial cells measure 6.0–8.0 µm diam. and 18–25 µm long. The perithallial cells gradually decrease in length distally, and the rounded apical cells measure to 7.0 µm diam. Crusts are variable in thickness, ranging from 320 to 830 µm. Cystoliths and trichocytes are absent. Tetrasporangial nemathecia are superficial and extensive, extending greater than 2.0 mm in extent and to 125 µm high. Tetrasporangia are cut off terminally from distal perithallial cells. The mature

tetrasporangia are cruciately divided, measuring to 260 µm long by 160 µm wide. Paraphysal cells are slender and measure to 2.0 µm diam. and become shorter distally, terminating in 1–3 spherical cells. Crusts are multicolored, with irregular patches of red, yellow, and orange.

Habitat and Comments: *Metapeyssonnelia mesophotica* was collected at depths of 49–70 m. The species was frequently found growing on presumably dead fragments of the scleractinian coral genus *Agaricia*.

As indicated above, the genus *Metapeyssonnelia* is characterized by interruptions in the regular "*Peyssonnelia*-like" organization of hypothallial cells that give rise to erect perithallial cells. The organizational interruption takes place differently in the new species compared with that originally described for the genus. In the new species, either a median-positioned perithallial cell cuts off a lateral that subsequently behaves as a hypothallus, or all cells of a given perithallial filament cut off branches laterally, and those filaments all arch dorsally and reach the dorsal surface (Figure 119C). Both of these organizational interruptions also take place in *Metapeyssonnelia tangerina* (Ballantine et al. 2014: figs. 3–7).

The new species was collected exclusively in water deeper than 49 m. All other members of the genus are presumably restricted to shallow-water environments. *Metapeyssonnelia mesophotica* also differs substantially from all recognized *Metapeyssonnelia* species (for which the character is known) in having substantially larger, to 260 µm long, tetrasporangia. In addition, the new species is easily differentiated from the three *Metapeyssonnelia* species that are currently recognized in Puerto Rico. The new species possesses superficial nemathecia, differing from *M. milleporoides*, which possesses immersed nemathecia and also possesses cystoliths. From *M. corallepida*, the new species differs in tetrasporangial initiation (borne terminally in the new species versus cut off laterally from the fertile paraphysal cell and also in lacking cystoliths). *Metapeyssonnelia tangerina* differs from the new species in a number of respects, including smaller colony size (to 30 cm in *M. tangerina* and to 80 cm in the new species). Tetrasporangial initiation in *M. tangerina* also differs from the new species similarly to that reported for *M. corallepida* above.

Two non-Caribbean species, *Metapeyssonnelia mexicana* (E.Y.Dawson) D.L.Ballant. et H.Ruiz (2011a) and *Metapeyssonnelia feldmannii* Boudouresque, Coppejans et Marcot (1976), are known from Pacific Mexico and from the Mediterranean, respectively. The former species, originally described as *Ethelia mexicana* E.Y.Dawson (1953), differs from the new species in being substantially smaller (2.0–3.0 cm in extent versus to 80 cm) and in possessing pluricellular elongate rhizoids versus short, nearly spherical rhizoids and depressed versus superficial tetrasporangial nemathecia. *Metapeyssonnelia mesophotica* differs from the generitype, *Metapeyssonnelia feldmannii*, in terms of calcification (hypobasal versus complete plus hypobasal) and the diameter of perithallial filaments (6.0–8.0 µm diam. versus 8.5–24 µm) and in the localized disruption of the "*Peyssonnelia*-like" morphology where an erect perithallus cell acts as a hypothallial filament versus the fountain-like cell arrangement (Boudouresque et al. 1976).

Metapeyssonnelia milleporoides D.L.Ballant. et H.Ruiz

FIGURE 120

Metapeyssonnelia milleporoides D.L.Ballant. et H.Ruiz 2011a: 47, figs. 1–8.

Puerto Rican Records: Ballantine and Ruiz 2011a; Reyes-Conteras et al. 2016.

Western Atlantic Distribution: Caribbean Mexico, Puerto Rico.

Type Locality: Mario Reef, La Parguera, Puerto Rico.

Thalli form large continuous crusts, to 20 cm in extent. The crusts possess light hypobasal calcification and have distinctive dark radial lines near the margins as well as finer striations. Crusts measure 500–660 µm thick and are closely adherent to the substratum, attached by unicellular rhizoids that may be spherical, measuring 8.0–13 µm in diameter, or elongate, to 27 µm in length. Perithallial cells are oriented parallel to each other, and cystoliths are present in the lower thallus. In section, coxal cells are highly variable in size and shape, measuring 15–30 µm in length and 25–40 µm in height, and normally cover the length of the bearing hypothallial cells. Coxal cells give rise to 2 files of perithallial cells. The perithallial cell files are closely laterally adherent, measuring 15–18 µm diam. and 20–43 µm in length proximally and 7.5–10 µm diam. and 10–18 µm in length at mid perithallus, and are 5–7.5 µm diam. at the apices. Perithallial cells are commonly dichotomously branched at mid perithallus. Hair mother cells measure to 15 µm diam. and 30–45 µm long. These specialized cells produce single small apiculate cells distally that do not penetrate through the outer mucilage layer. Crusts at their margin have multiple hypothallial cells that produce both inferior and superior files of perithallial cells. Nemathecia are mostly sunken, slightly extending above the level of the adjacent

FIGURE 120. *Metapeyssonnelia milleporoides*. In situ photograph, Laurel Reef, growing on *Millepora complanata* Lamarck. Field is approximately 0.3 m.

perithallial files of cells. Spermatangia occur in sori to 50 µm high. Female gametophytes are unknown. Tetrasporangial nemathecia measure to 1.9 mm in extent and 120 to 175 µm high. Tetrasporocytes are cut off from a basal paraphysal cell and measure to 25 µm diam. and 65 to 100 µm long. Algae are brownish with reddish highlights, becoming dark reddish purple below.

Habitat and Comments: *Metapeyssonnelia milleporoides* is found in shallow water, typically epizootically on the hydrocoral *Millepora complanata* and, to a lesser extent, *Porites* species. Overgrowth by *M. milleporoides* ultimately results in death of the coral. See comments on allelopathy under *Metapeyssonnelia corallepida*.

Metapeyssonnelia tangerina D.L.Ballant., C.Lozada-Troche et H.Ruiz

FIGURE 121

Metapeyssonnelia tangerina D.L.Ballant., C.Lozada-Troche et H.Ruiz 2014: 198, figs. 1–11.

Puerto Rican Records: Ballantine et al. 2014.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Cabo Rojo lighthouse, southwestern corner of Puerto Rico.

Crustose thalli measure to 30 cm in extent and are variable in thickness, up to 950 µm and more than 25 cells thick. Crusts possess dark radial markings and are closely appressed to their substratum, possessing unicellular rhizoids, from 50 to 100 µm long. Calcification is hypobasal, and the hypothallus cells are arranged in fan-shaped arrangements when viewed ventrally. Perithallial coxal cells nearly cover the bearing hypothallial cells or are cut off from the distal ends of hypothallial cells. The coxal cells produce 1 or 2 erect lower perithallial cells. Trichocytes (hair mother cells) are common in the upper perithallus. Nemathecia are raised above the crust surface. Carposporangia are cut off in occasionally branched chains of 2–4 sporangia that are up to 50 µm broad and to 80 µm long. Tetrasporangia measure to 40 µm broad and to 120 µm long. Algae are bright orange in color.

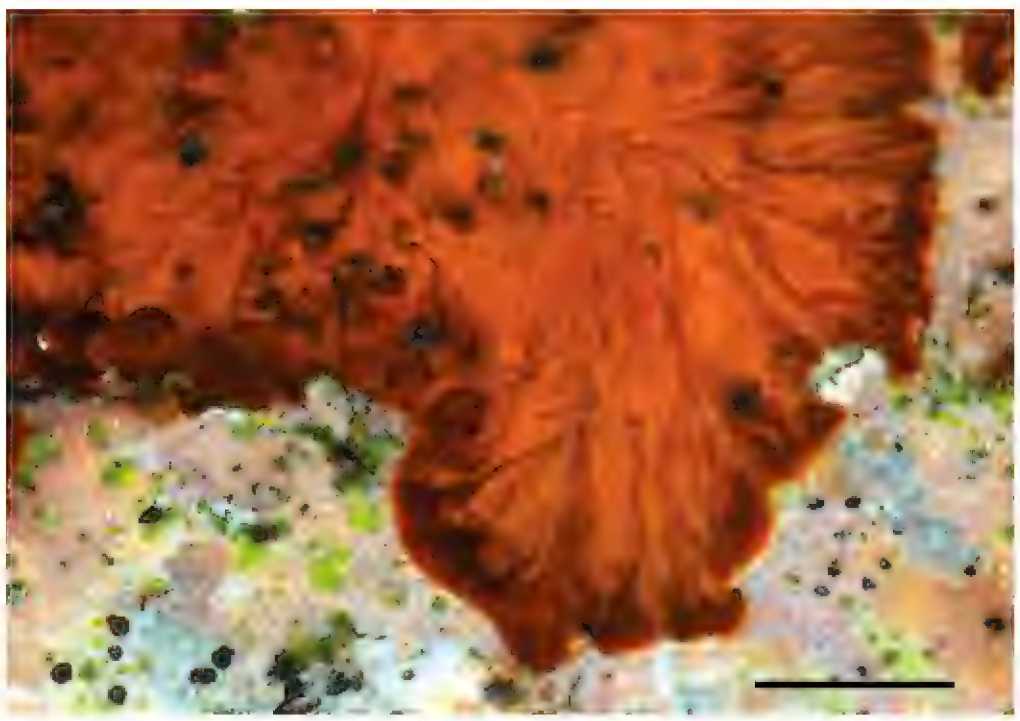

FIGURE 121. *Metapeyssonnelia tangerina*. In situ photograph, entrance to Bahia Sucia, Cabo Rojo lighthouse, 2.0 m. Scale bar = 10.0 cm.

Habitat and Comments: *Metapeyssonnelia tangerina* is common in shallow reef habitats in southwest Puerto Rico. The species is typically found on dead corals in fore-reef, moderately high wave energy environments.

Mucopeyssonnelia D.L.Ballant. et H.Ruiz gen nov.

Mucopeyssonnelia D.L.Ballant. et H.Ruiz gen. nov.

Generitype: *Mucopeyssonnelia westii* D.L.Ballant., H.Ruiz et J.N.Norris herein.

Etymology: The generic epithet refers to the mucous nature of the *Peyssonnelia*-like alga.

Description: Dorsiventrally organized thalli are crustose and possess hypobasal calcification. The hypothallus consists of a network of filaments composed of axes of large veinlike cells (primary hypothallus) that give rise to smaller-diameter filaments (secondary hypothallus) that are cut off at acute or 45° angles such that they are initially parallel to each other. The primary hypothallus filaments, when observed from below, are irregularly unilaterally branched. Secondary hypothallial files ultimately form flabellate arrangements The primary and secondary hypothallus filaments collectively form a single prostrate hypothallial layer. All hypothallial cells produce a single coxal cell that gives rise to files of erect perithallial cells. Perithallial cells are not laterally coherent and are embedded within a copious mucilage. The apices of perithallial filaments are covered by a membrane-like structure, and groups of perithallial filaments frequently arch toward a common point. Reproductively, only male gametophytes are known; spermatangia are cut off in small irregular clusters by perithallial apical cells.

Comments: *Mucopeyssonnelia* is easily placed into the Peyssonneliaceae by its possession of a hypothallus whose cells gives rise to a coxal cell that, in turn, gives rise to perithallial filaments. However, the new genus is unique among Peyssonneliaceae genera in having large prostrate filaments of veinlike cells (the primary hypothallus) that produce second-order hypothallus filaments, the joining of surface cells from nearby perithallial filaments, the at least partial membranous covering of perithallial cells, and the extreme mucilaginous nature of the thallus.

Mucopeyssonnelia westii D.L.Ballant., H.Ruiz et J.N.Norris sp. nov.

FIGURE 122

Mucopeyssonnelia westii D.L.Ballant., H.Ruiz, et J.N.Norris sp. nov., Fig. 122A–E.

Holotype: DLB6180 (US Alg. Coll. 238342), seaward Margarita Reef, 24 m, Coll. DLB, HR, 29.iv.2004.

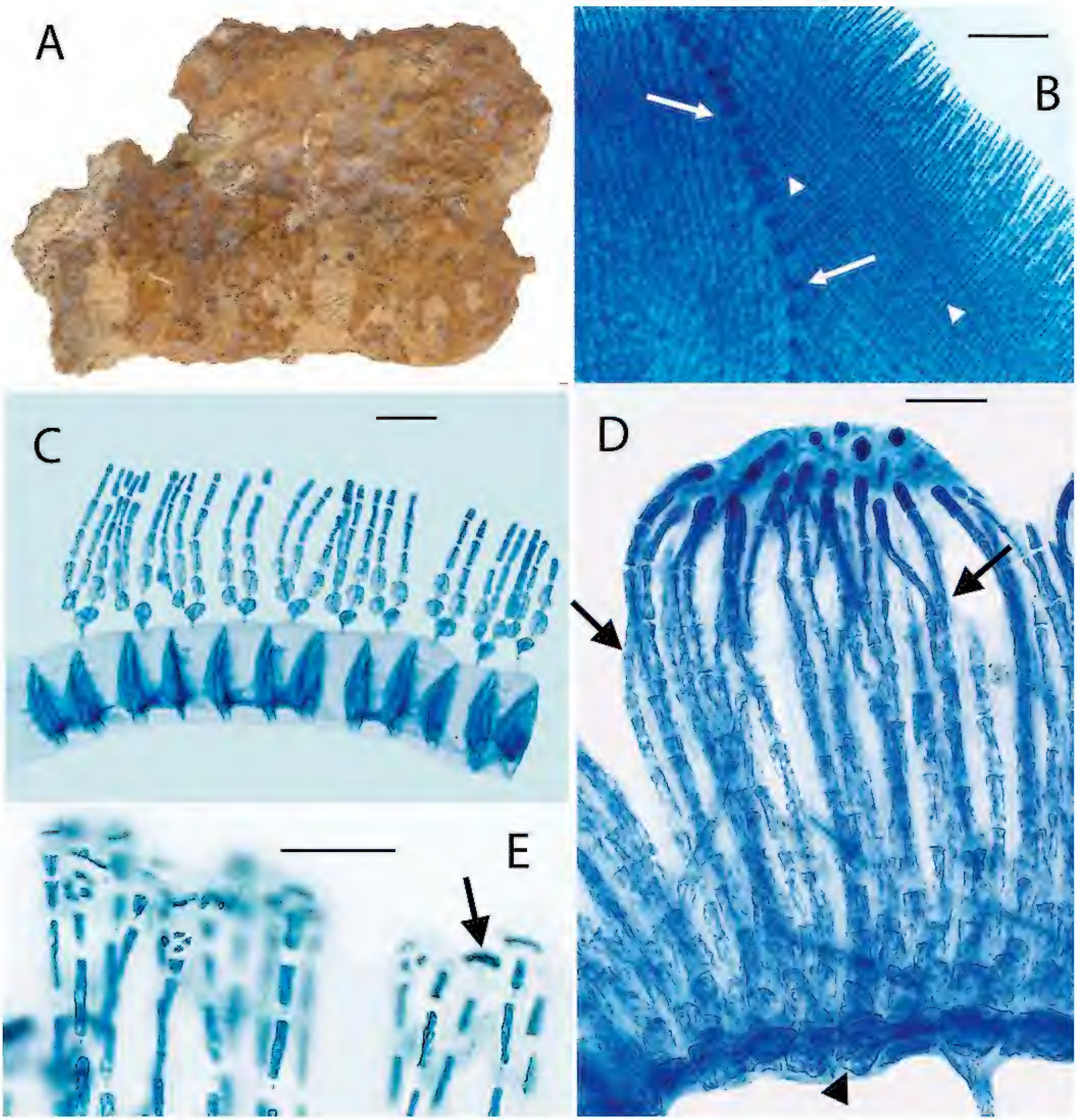

FIGURE 122. *Mucopeyssonnelia westii*. (A) DLB6180, holotype, seaward Margarita Reef, 24 m. Specimen = 4.7 cm across. (B) DLB6180, ventral view showing large primary hypothallial filament (arrows) with lateral secondary hypothallial filaments (arrowheads). Scale bar = 100 µm. (C) DLB6180, primary hypothallial filament with dorsally oriented perithallial filaments. Scale bar = 50 µm. (D) DLB7334, secondary perithallial filament with erect-growing perithallial filaments. Arrows denote perithallial filaments, and the arrowhead denotes a secondary hypothallus cell. Scale bar = 50 µm. (E) DLB7974, spermatangia cut off from apical perithallial cells. Arrow denotes membrane remnant. Scale bar = 25 µm.

Isotype: U.S. Algal Coll. 238358.

Paratypes: DLB7334 (US Alg. Coll. 238357), edge of insular shelf offshore from La Parguera, "Weinberg" Reef, Coll. HR, 11.iii.2008, 50 m; DLB3138 (US Alg. Coll. 235419), South of St. Thomas, U.S. Virgin Islands (18.5°N, 64.48°W), dredged on Oregon II, 11.viii.1987, 44 m; DLB3363 (US Alg. Coll. 238356), 1.5 km seaward Media Luna Reef, Coll. DLB, 1.xi.1988, 17 m; DLB7454 (US Alg. Coll. 236325), edge of insular shelf offshore from La Parguera, "Black Wall" Reef, Coll. HR,15.iv.2008, 57 m; DLB8043, Vieques ("El Seco"), Coll. HR, 17.i.2010, 70 m.

Western Atlantic Distribution: Puerto Rico, St. Thomas, U.S. Virgin Islands.

Etymology: The species epithet, *westii*, is in honor of our friend and colleague John A. West (University of Melbourne) in recognition of his numerous phycological studies and publications.

Description: Crustose thalli are greater than 6.0 cm in extent, 200–400 µm thick, and very mucose. Large veinlike primary hypothallus filaments are composed of cells to 25–50 µm long and 30–125 µm diam. Secondary hypothallus filaments, cut off laterally from the primary hypothallus, possess cells that measure 9.0–30 µm long, 10–18 µm wide, and 10–20 µm high. Multicellular rhizoids are cut off from the anterior ends of hypothallial cells, measuring 8.0–10 µm in diameter and to 400 µm long. Hypothallial cells give rise to, at their middle, a single boot-shaped or ovate coxal cell, ~15 µm wide and 27 µm high. Coxal cells give rise mostly to 2 files of erect perithallial cells. Occasionally one of the proximal branch cell redivides, such that 3 erect filaments are generated per coxal cell. The perithallial filaments are 6.0–14 cells in length, and perithallial cells measure 5.0–10 µm diam. and 25–40 µm long. Periaxial cells decrease in length and diameter distally; apical cells measure 5.0 µm in diameter. Male gametophytes cut off small clusters of spermatangia surrounding the perithallial apical cells.

Habitat and Comments: *Mucopeyssonnelia westii* is the generitype. In Puerto Rico, the new species is apparently rare and is highly inconspicuous. *Mucopeyssonnelia* has been collected at 17 m depth in the offshore algal plains as well as deep coral reef habitats to 57 m. The Caribbean report of "*Erthryodermis haematis* (Hollenberg) Denizot (1968; 223, figs. 187–192)" was based on an incorrect identification by Littler and Littler (2000: 84–85), and their material is now recognized to be *Mucopeyssonnelia westii*.

Peyssonnelia Decne.

Peyssonnelia Decne. 1841: 168.

Thalli are normally crustose with hyobasal calcification. Anatomically, the crusts are composed of a single-cell-thick hypothallus that is prostrate on the substratum and a perithallus of dorsally directed filaments. Hypothallus filaments may be arranged either in a fanlike arrangement or as parallel files. The crusts are strongly adherent or loosely attached. Thallus surfaces sometimes possess concentric and/or radial lines. Thalli are attached by unicellular or multicellular rhizoids. Reproductive structures occur in nemathecia, among specialized filaments, paraphyses; however, spermatangial sori lack them. Carpogonial branches are 2–4-celled. Auxiliary cells are intercalary, borne laterally on paraphyses. Carposporangia occur in simple or branched chains. Tetrasporangia are regularly to irregularly cruciately divided. Eighty-nine species of *Peyssonnelia* are currently recognized; with the addition of *P. tenuicrusta* (below), 10 species occur in Puerto Rico.

KEY TO THE *AGISSEA* AND *PEYSSONNELIA* SPECIES OF PUERTO RICO

1. Crustose thalli are largely free from their substratum or free at their margins 2
   Thalli mostly adherent to their substratum. 3
2. Blades with iridescent blue margins when living. . . . . *P. iridescens*
   Blades not iridescent. . . . . *P. tenuicrusta*
3. Crusts with polyflabellate hypothallial filaments 4
   Crusts with hypothallial filaments in parallel rows. 5
4. Thalli completely calcified; producing thick accretions due to overgrowth of crusts. . . . . *P. imbricans*
   Thalli with hypobasal calcification; crusts do not produce additional crusts dorsally; thalli 100–500 µm thick; thalli frequently streaked with green and maroon colors . . . . . *P. boergesenii*
5. Frequent lateral fusions occur between adjacent perithallial cells . . . . . *P. incomposita*
   Cells of lateral perithallial files do not fuse. 6
6. Perithallus appearing to be stratified when viewed in section . . . . . *P. stratosa*
   Perithallus not appearing to be stratified in section 7
7. Crust generally less than 150 µm thick. 8
   Crust generally greater than 200 µm thick 9
8. Crust exhibiting distinct radial markings; tetrasporangia reaching 250 µm in length . . . . . *P. gigaspora*
   Crust without radial markings; tetrasporangia maximally to 100 µm in length . . . . . *A. inamoena*
9. Crusts to 640 µm thick; tetrasporangia to 170 µm in length . . . . . *P. flavescens*
   Crusts to 220 µm thick; tetrasporangia to 53 µm in length . . . . . *P. conchicola*

Peyssonnelia boergesenii Weber-Bosse

FIGURE 123

Peyssonnelia boergesenii Weber-Bosse in Børgesen 1916: 137: figs. 142–145.
Puerto Rican Records: Ballantine and Ruiz 2005; Ruiz and Ballantine 2009; Ballantine et al. 2016b.
Western Atlantic Distribution: Belize, Caribbean Mexico, Cuba, Puerto Rico, U.S. Virgin Islands, Brazil.
World Distribution: See Guiry and Guiry 2024.
Type Locality: White Bay, St. Croix, U.S. Virgin Islands.

Crustose thalli, ~500 µm thick, are completely adherent to the substratum and possess conspicuous radiating veinlets. Thalli are attached by abundantly produced, occasionally branched multicellular rhizoids, 23 µm diam. and 1.0 mm long. The hypothallus filaments are composed of cells, to 38 µm long and to 39 µm high, that are variable in size and shape. The hypothallus filaments occur in small fanlike arrangements. Coxal cells are boot shaped and typically give rise to 2 files of cells. Perithallial cells, 20–40 µm diam. and 30–40 µm tall proximally, decrease to 10–13 µm diam. and 10 µm tall. Ascending perithallial filaments either are deflected at a 60° angle or are nearly perpendicular. Reproductive nemathecia are ~260 µm thick with slender elongate paraphysal cells below, becoming short above. Gametophytes are presumably monoecious. Carpospores, ~20 µm diam., are cut off in chains of 4. Tetrasporangia, up to 50 µm diam. and 160 µm long, are cut off laterally from basal paraphysal cells. Algae are multicolored, typically with a greenish background with broad irregular maroon or brownish-red streaks.

Habitat and Comments: *Peyssonnelia boergesenii* is usually considered to be a shallow-water species (e.g., Taylor 1960). In Puerto Rico the species is also known from very shallow water, 0.5 m depth, and in much deeper water down to 61 m depths (Ballantine and Ruíz 2005). [Additional illustrations: Guimarães and Fujii 1999: figs. 16–22; Littler and Littler 2000: 87; Ballantine and Ruiz 2005: figs. 1, 5–7.]

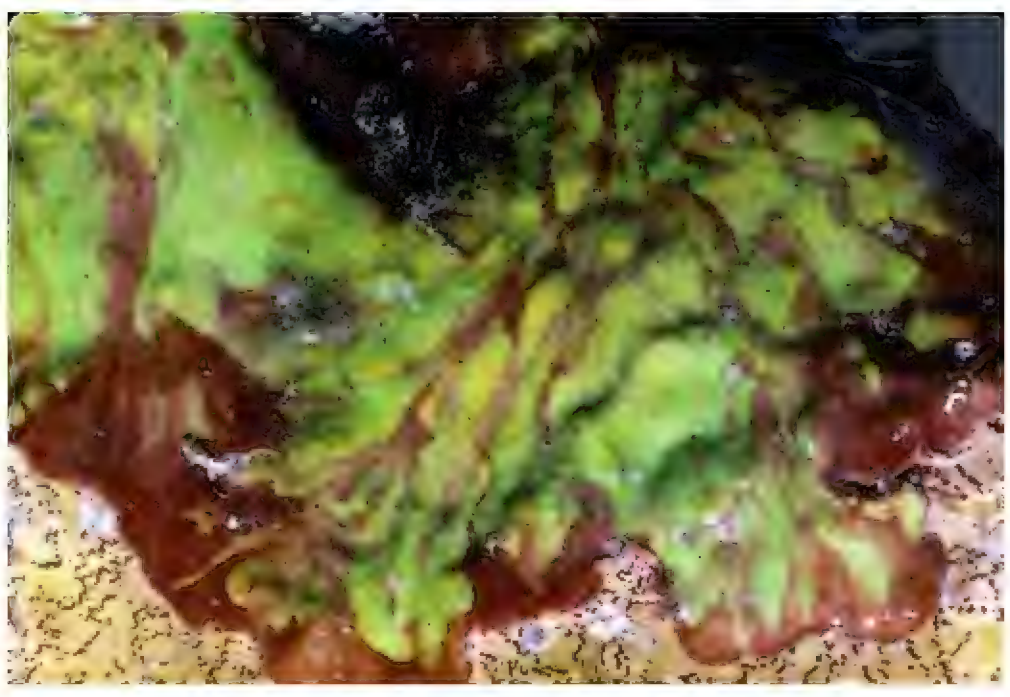

FIGURE 123. *Peyssonnelia boergesenii*. DLB5854, live specimen, edge of insular shelf, off La Parguera, 20 m, overgrowing *Peyssonnelia flavescens*. Field is approximately 5.0 cm.

Peyssonnelia conchicola Picc. et Grunow in Picc.

Peyssonnelia conchicola Picc. et Grunow in Piccone 1884: 317, pl. VII: figs. 5–8.
Puerto Rican Records: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002a.
Western Atlantic Distribution: Costa Rica, United States (North Carolina), Cuba, Puerto Rico, Martinique, U.S. Virgin Islands, Colombia.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Massawa, Eritrea, Ethiopia.

Crustose thalli, 1.0–3.0 cm diam., are strongly adherent to the substratum, attached by numerous short rhizoids. Calcification is hypobasal. The hypothallus (when viewed from below), consists of straight parallel filaments, 7.0–14 µm diam. and 22–44 µm long. The hypothallus cells measure to 28 µm high in sectional view. Coxal cells give rise to generally 3 perithallial cells that are cut off obliquely from the hypothallus. The proximal cells are 2–3 times taller than broad; the distal cells are half as tall as broad. Vegetative crusts are thin, to 220 µm thick, with ascending perithallial filaments 3–6 cells long. Gametophytes are monoecious, with spermatangia and carpogonia occurring in the same nemathecia. Nemathecial paraphyses are subclavate. Tetrasporangia occur in immersed nemathecia and measure 23–35 µm diam. and ~80–100 µm long. Algae are red purple in color.

Habitat and Comments: *Peyssonnelia conchicola* is little known in Puerto Rico. The species occurrence in Puerto Rico is based on the report by Díaz-Piferrer (1963) of a specimen (FP-DB 3085, in MSM) from the lower intertidal at Ballena Bay, Guánica. [Illustrations: Schneider and Searles 1991: figs. 295–297; Littler and Littler 2000: 189.]

Peyssonnelia flavescens D.L.Ballant. et H.Ruiz

FIGURE 124

Peyssonnelia flavescens D.L.Ballant. et H.Ruiz 2005: 331–333, figs. 2–4, 8–15.
Puerto Rican Records: Ballantine and Ruiz 2005; Ruiz and Ballantine 2009; Ballantine et al. 2016b; Sherman et al. 2023.
Western Atlantic Distribution: Puerto Rico, St. Eustatius.
Type Locality: Edge of insular shelf offshore of La Parguera, Puerto Rico.

Crusts reach up to 30 cm in extent and are closely adherent to the substratum. The crusts are variable in thickness, measuring 6–12 cells in length and 310–640 µm. Simple rhizoids, cut off from the anterior ends of the hypothallial cells, are unicellular and measure to 450 µm in length. Calcification is limited to the hypothallial region. The hypothallus forms straight files

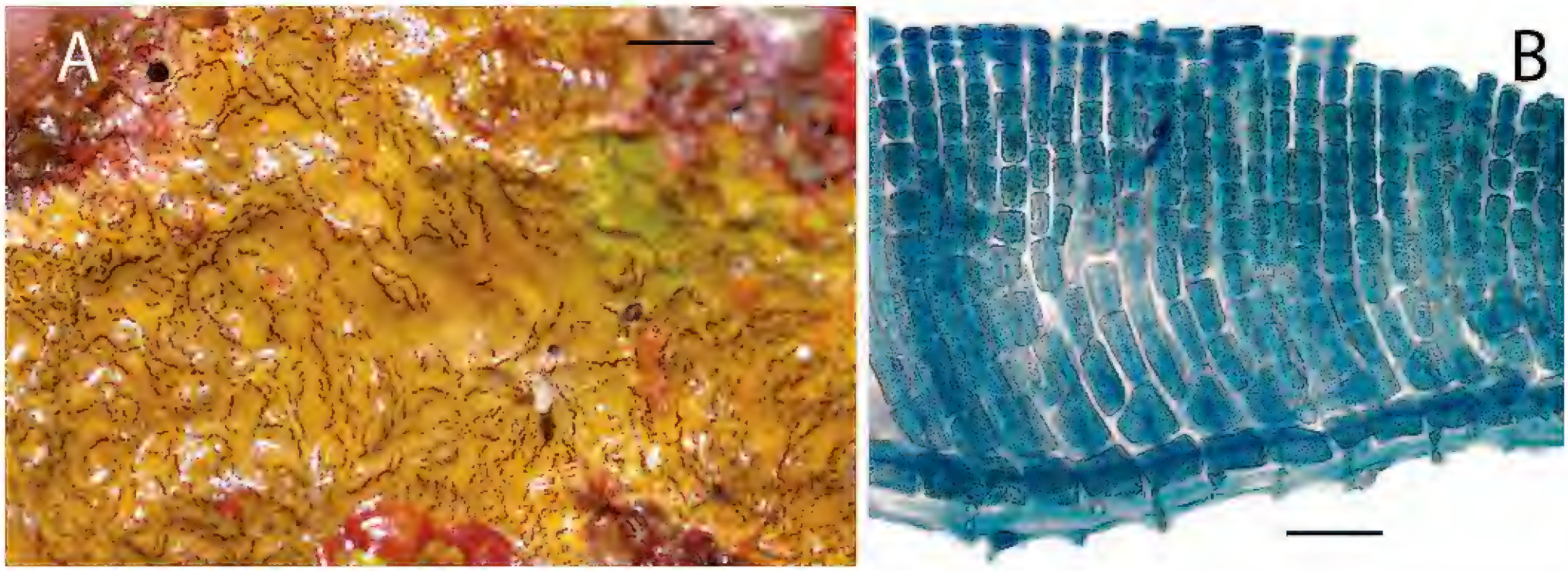

FIGURE 124. *Peyssonnelia flavescens*. (A) In situ photograph, edge of insular shelf, off La Parguera, 18 m. Scale bar = 1.0 cm. (B) DLB5883, photomicrograph, radial transverse section. Scale bar = 100 µm.

of cells. The cells measure 25–40 µm in length and 18–25 µm in height when viewed in radial transverse section. Coxal cells give rise to 2 files of ascending perithallial cells that may rebranch once and become progressively narrower and shorter distally. The proximal perithallial cells are nearly square to rectangular and measure 30–35 µm in length, 25–35 µm in height, and 10–12.5 µm diam. The perithallial cells are cut off at angles from 60° to nearly perpendicular to the plane of the hypothallus. Gametophytes are apparently dioecious, although female algae are unknown. Spermatangia occur in nemathecial sori to 40 µm high. Spermatangial mother cells cut off spermatangia in seriate chains distally. Ovate tetrasporangia, 80 µm diam. and to 170 µm long, are cut off laterally from an enlarged basal paraphysal cell. Shallow-water crusts are brownish orange in color with irregular yellowish portions and with dark maroon lines and spotting. Deeper-water crusts are bright yellow, orange yellow, or reddish yellow in color with irregular reddish or dark lines and spotting.

Habitat and Comments: *Peyssonnelia flavescens* has been collected in shallow-water habitats, at intermediate depths at a mid-shelf coral reef site (Media Luna Reef), and in deeper coral reef habitats. Although never abundant, the species is conspicuous due to its coloration and large size.

Peyssonnelia gigaspora D.L.Ballant. et H.Ruiz

FIGURE 125

Peyssonnelia gigaspora D.L.Ballant. et H.Ruiz 2010: 539, figs. 3, 4, 14–20.

Puerto Rican Records: Ballantine and Ruiz 2010; Ballantine et al. 2016b; Sherman et al. 2023.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Edge of insular shelf ("El Hoyo"), offshore from La Parguera, Puerto Rico.

Crustose thalli, closely appressed to the substratum, measure up to 12 cm across, although they are normally half that size. Crusts typically average 130 µm and 7 cells in thickness. When thalli grow over a depression in the substratum, they maintain their upper surface at the same level as the previous growth and, under these conditions, may reach 200 µm and 15 cells thick. Calcification is hypobasal. Hypothallial filaments are arranged in regular parallel rows. In radial transverse section, hypothallial cells are cuboid or rectangular and measure 30–50 µm long and up to 30 µm high. These cells cut off unicellular rhizoids up to 300 µm long from their distal ends. Perithallial coxal cells are typically cut off perpendicularly to the bearing hypothallial cell, however, sometimes at an angle of 70°. The perithallial coxal cell gives rise to 2 filaments; these are initially up to 13.5 µm long and 6.0 µm in diam., becoming somewhat shorter distally. Perithallial rows are occasionally dichotomously divided above the level of the coxal cells. Apical perithallial cells are dome-shaped and measure to 5.3 µm diam. and from 3.8 to 4.5 µm high. Hair cells are not produced. Tetrasporangia are present in irregularly positioned nemathecia that mostly measure up to 2.0 mm across. These may become confluent, resulting in nemathecia up to 9.0 mm long and 2.0 mm in width. The nemathecia extend to a height of 250 µm above the level of surrounding vegetative cells. Nemathecial filaments are extremely slender, ~1.5–2.5 µm in diameter, and terminate in 2 expanded cells. Tetrasporangia are cut off by the basal nemathecial cell. At maturity, the unusually large, cruciately divided tetrasporangia are elongate-oval, measuring up to 105 µm diam. and 175–250 µm long. Algae are tan colored with striking purple radial striations.

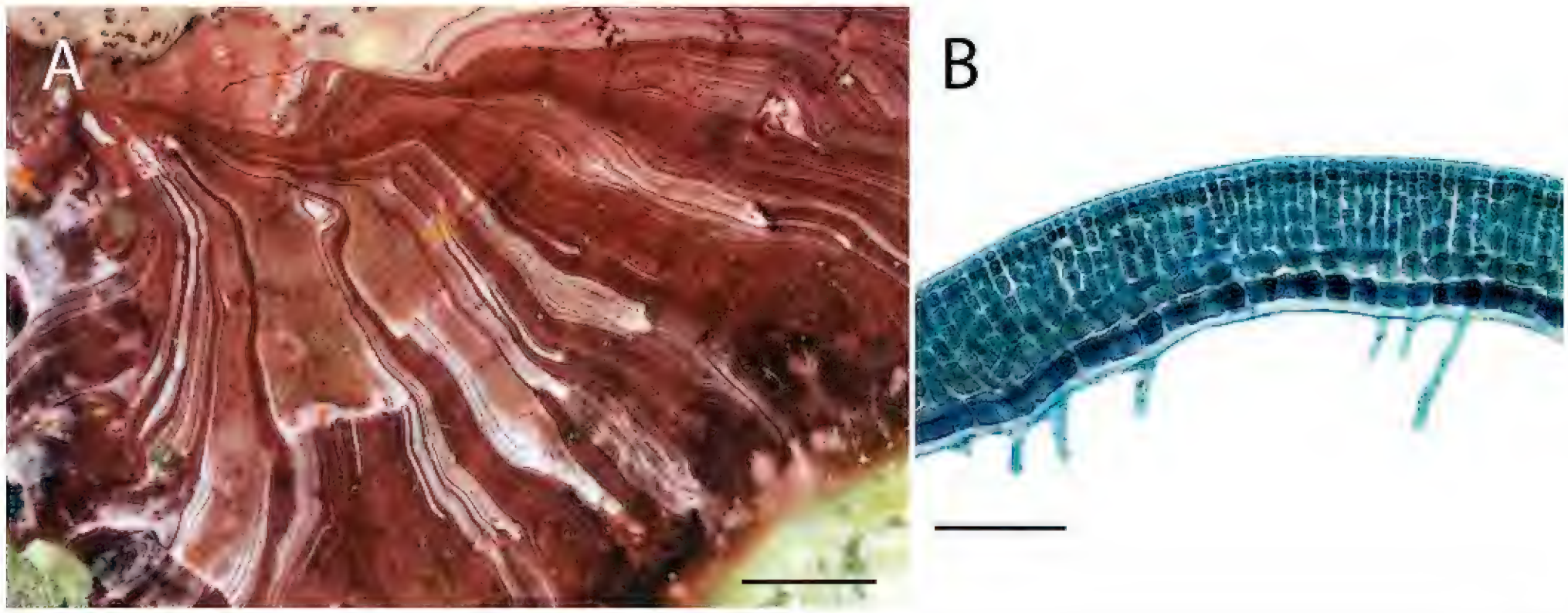

FIGURE 125. *Peyssonnelia gigaspora*. (A) DLB7637, live specimen, habit of the holotype, edge of insular shelf, off La Parguera, 70 m. Scale bar = 2.0 mm. (B) Photomicrograph, radial transverse section. Scale bar = 100 µm.

Reddish-brown spots may be arranged in concentric rings or are irregularly distributed.

Habitat and Comments: Currently known only in Puerto Rico, the endemic *Peyssonnelia gigaspora* is a deepwater species, occurring from 46 to 91 m depths.

Peyssonnelia imbricans D.L.Ballant. et H.Ruiz

FIGURE 126

Peyssonnelia imbricans D.L.Ballant. et H.Ruiz 2007: 72.

Peyssonnelia imbricata D.L.Ballant. et Ruiz 2006: 431, figs. 1–17, nom illeg.

Misapplied Name: Cruoriella armorica P.Crouan et H.Crouan 1858.

Puerto Rican Records: As *Peyssonnelia imbricans*: Ballantine and Ruiz 2007. As *Peyssonnelia imbricata:* Ballantine and Ruiz 2006. As *Cruoriella armorica:* Ballantine et al. 2000; Ballantine and Aponte 2002a.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Cayo Aurora, Guánica, Puerto Rico.

Completely calcified thalli produce small imbricating crusts, 4.0–11 mm broad by 3.0–10 mm long. Individual crusts are 6–7 cells in height and 110–180 µm thick. The entire encrustation may reach 40 cm in extent. Young crusts are produced vegetatively from the dorsal surface of parent crusts. Thalli produce thick accretions through the overgrowth of blades with as many as 5 layers retaining pigmentation and with total accretion to 8.0 mm thick. The crusts possess distinct radial lines. The hypothallus, consisting of filaments in flabellar arrangements, possess simple unicellular spherical rhizoids that are cut off from the anterior ends of the hypothallial cells. In radial transverse section, hypothallial cells measure 34–48 µm long and to 27. 5 µm high. Coxal cells, 35–40 µm long and 30–35 µm high, are cut off from near the anterior end of the hypothallial cells at angles from 50° to 60°. The coxal cells give rise to 2 ascending files of perithallial cells; the perithallial cells measure 17–25 µm diam. and 20–35 µm high. Hair mother cells are occasionally present in the distal perithallus. Gametophytes are monoecious. Spermatangial nemathecia are inconspicuous and bear spermatangia in simple chains. Carpogonial branches, cut off from basal paraphysal cells, are 2 cells long, and nearly all paraphysal filaments of female nemathecia cut off 4- or 5-celled auxiliary cell branches. Carposporangia mostly occur in chains of 3, with mature carposporangia measuring to 30 µm diam. and 45 µm long. Algae are brown to orange in color.

Habitat and Comments: *Peyssonnelia imbricans* occurs in coral reef habitats, forming rhodoliths, and on coral rubble and is epiphytic on mangroves, *Rhizophora mangle*. Ballantine et al. (2006) described the entity as a new species, *Peyssonnelia imbricata*. Recognizing it was a later homonym of *P. imbricata* Kütz. (1849), Ballantine and Ruíz (2007) renamed the taxon to be *P. imbricans*.

Peyssonnelia incomposita D.L.Ballant. et H.Ruiz

FIGURE 127

Peyssonnelia incomposita D.L.Ballant. et H.Ruiz 2011b: 21, figs. 1–10.

Puerto Rican Records: Ballantine and Ruiz 2011b; Ballantine et al. 2016b; Sherman et al. 2023.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Edge of insular shelf ("Weinberg") off La Parguera, Puerto Rico.

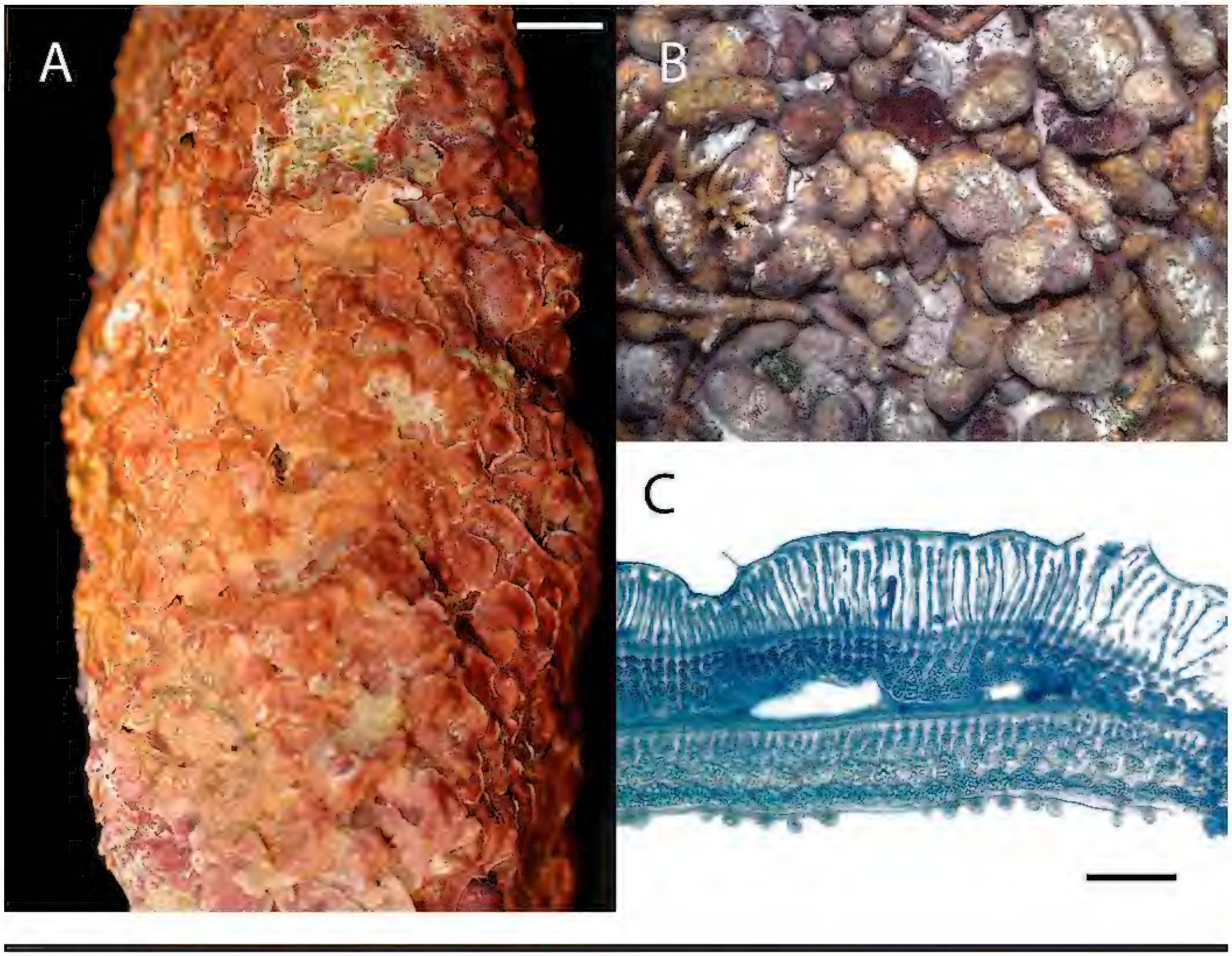

FIGURE 126. *Peyssonnelia imbricans*. (A) DLB6854, holotype specimen, epiphytic on *Rhizophora*, Cayo Aurora Reef, 0.5 m. Scale bar = 1.0 cm. (B) *Peyssonnelia imbricans* rhodoliths, leeward Media Luna Reef, 1.5 m. Field is approximately 40 cm. (C) Photomicrograph of holotype, radial transverse section showing secondary crust originating from parent crust and bearing a tetrasporangial sorus. Scale bar = 100 µm.

Thalli, without concentric or longitudinal striations, measure to 30 cm across. The crusts are closely appressed to the substratum, and calcification is hypobasal. Hypothallial filaments are arranged in more or less parallel files. The hypothallial cells, viewed in radial section, are square to rectangular in shape, measuring 15–22.5 µm long and 11–15 µm high. Unicellular rhizoids average approximately 100 µm in length and are produced from the proximal end of hypothallial cells. Coxal cells, 10–13 µm long and 8–10 µm high, are cut off from the center of the bearing hypothallial cell; however, they cover only approximately half the length of the cell. The coxal cell generally gives rise to a single, less commonly 2, assurgent filament(s). Perithallial cells measure to 12.5 µm in breadth below, decreasing to 7.5 µm distally. The crust is typically 60–75 µm and 8 cells thick. Hair cells are not produced. Abundant cell fusions between adjacent perithallial cells as well as between cells of adjacent perithallial filaments at different tier levels results in a disorganized appearance when viewed in section. Gametophytes are unknown. Tetrasporangia are produced in large nemathecia that extend up to 125 µm above the level of surrounding vegetative cells. Elongate-oval, cruciately divided tetrasporangia, up to 30 µm diam. and 80 µm long, are cut off directly from proximal nemathecial cells. Algae are reddish-orange encrustations that are highlighted with bright yellow markings.

Habitat and Comments: *Peyssonnelia incomposita* is an exclusively deepwater species, having been collected from 50 to 73 m in depth, currently known only from Puerto Rico. *Peyssonnelia incomposita* may prove to be related to the genus *Seiria* K.R.Dixon (in Huisman 2018) in that *Seiria* is characterized by

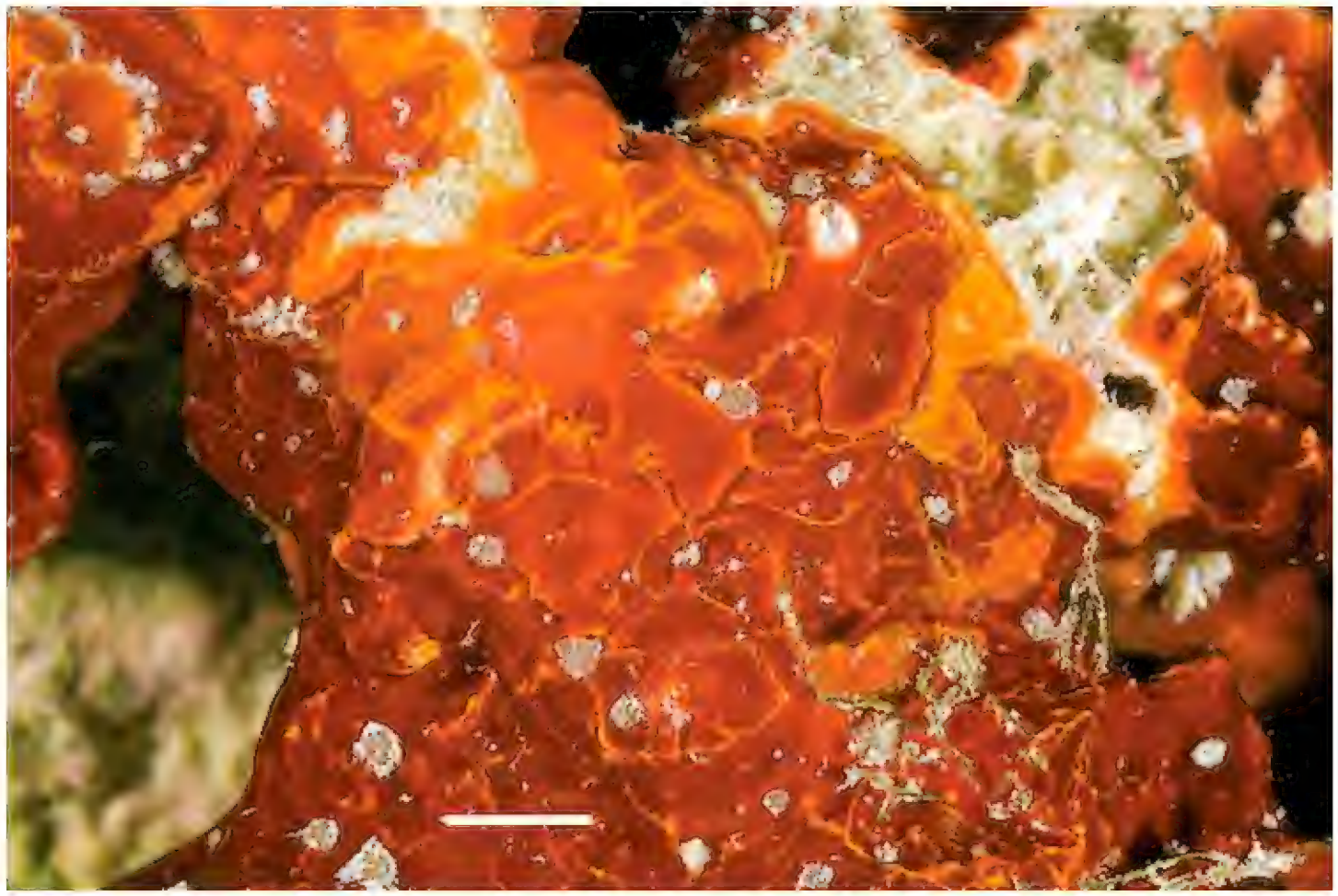

FIGURE 127. *Peyssonnelia incomposita*. DLB7777, holotype specimen, edge of insular shelf of La Parguera, 50 m. Scale bar = 1.0 cm.

cell fusions among perithallial cells. In *Seiria*, tetrasporangia are reported to be borne by basal paraphysal cells and are borne from proximal nemathecial cells. Nevertheless, this character is variable in *Peyssonnelia*.

Peyssonnelia iridescens D.L.Ballant. et H.Ruiz

FIGURE 128

Peyssonnelia iridescens D.L.Ballant. et H.Ruiz 2010: 538, figs. 1, 2, 5–13.

Puerto Rican Records: Ballantine and Ruiz 2010; Ballantine et al. 2016b; Sherman et al. 2023.

Western Atlantic Distribution: Puerto Rico.

World Distribution: See Guiry and Guiry (2024).

Type Locality: Edge of insular shelf ("Weinberg") off La Parguera, Puerto Rico.

Bladelike thalli measure up to 6.0 cm in width and length, with new blades developing as lobes from the margins; entire colonies measure up to 10 cm across. The blades are loosely attached, possessing numerous, long unicellular rhizoids, averaging ~100 µm in length (to 330 µm). Calcification is light and strictly hypobasal. Hypothallial filaments are arranged in regular parallel files. Hypothallial cells measure up to 40 µm long and to 10 µm high. Coxal cells, often triangular in shape and measuring 25 µm long by 25 µm high, are cut off from the distal half of the bearing hypothallial cell. Coxal cells give rise to 2 assurgent filaments, 6.0–7.0 µm diam., at angles of 70°–80°. The crust is typically 5(–6) cells and up to 100 µm thick. Hair cells are not produced. Gametophytes are presumably monoecious, although male structures are unknown. Female nemathecia are linear, up to 15 mm long and 2.0 mm wide, and superficial. Carpogonial branches are 2–3 cells long and are cut off from perithallial apical cells. Auxiliary cell branches are mostly 4-celled and are also cut off from perithallial apical cells. Carposporangia are formed in simple or subdichotomously branched chains of 3 or 4, originating from connecting filaments. Individual carposporangia are mostly spherical or squarish and measure 25–30 µm in largest dimension. Tetrasporophytes are rare, with tetrasporangia occurring in nemathecia that extend up to 130 µm above the level of surrounding vegetative cells. Elongate oval tetrasporangia, 53 µm diam. and 250 µm long, are cruciately divided. Algae are typically orange or reddish blades with faint reddish longitudinal striations. The blade margins are commonly strikingly iridescent blue.

Habitat and Comments: *Peyssonnelia iridescens* is an exclusively deepwater species, having been collected to 87 m depth along the south Puerto Rico shelf edge. Due to its iridescence and loosely attached habit, the species is a visually conspicuous element of the Puerto Rican mesophotic community.

Peyssonnelia stratosa D.L.Ballant. et H.Ruiz

FIGURE 129

Peyssonnelia stratosa D.L.Ballant. et H.Ruiz 2012: 236, figs. 1–10.

Puerto Rican Records: Ballantine and Ruiz 2012.

Western Atlantic Distribution: Puerto Rico.

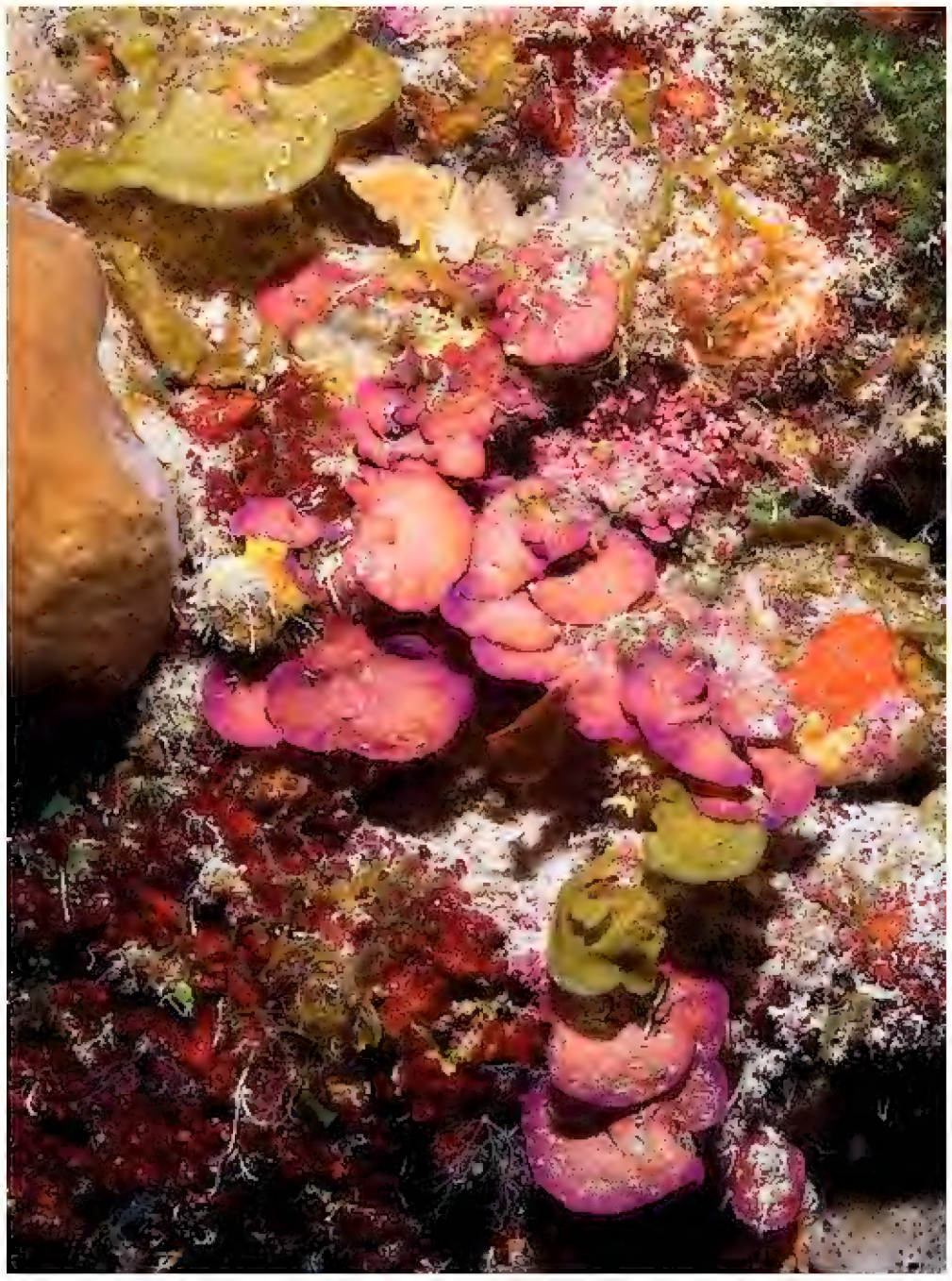

FIGURE 128. *Peyssonnelia iridescens*. In situ photograph, edge of insular shelf, 80 m. Field is approximately 15 cm.

Type Locality: West of Cabo Rojo lighthouse, Cabo Rojo, Puerto Rico.

Crustose thalli possess prominent radial striations and are largely free at their margins. The hypothallus is arranged in slightly curved parallel files. Hypothallial cells are squarish, 30–35 µm in length and height, and give rise to elongate, 400 µm long, rhizoids at their anterior ends. Coxal cells normally give rise to 2 cells, and one of these (the anterior one) branches, resulting in 2 files of perithallial cells, and the other remains undivided until near the dorsal surface, where it commonly divides dichotomously. Proximal cells of the perithallial filaments measure to 15 µm broad and to 35–40 µm high. At approximately the lower third of the perithallus, each of the regular files of perithallial filaments is typically interrupted by the presence of a single short cell, 5.0–10 µm long, above and below which the cells are to ~30 µm long and ~12 µm broad. The resultant appearance (when viewed in section) is a perithallus in 2 layers. Occasionally, production of short perithallial cells more distally gives rise to the appearance of 3 tiers. Apical perithallus cells are dome shaped and measure 10 µm diam. The perithallus is composed of 6 to 10 cells, and the entire crust ranges from 100 to 230 µm in thickness. Occasional hair mother cells are observed in the upper perithallus, measuring 16 µm in width and 35 µm long. Gametophytes are unknown. Tetrasporangia occur in discrete nemathecia that measure to 130 µm in height. Cruciately divided tetrasporangia, 65 µm diam. and 160–195 µm long, are cut off laterally from the proximal nemathecial cell. Algae are yellowish to beige in color.

Habitat and Comments: *Peyssonnelia stratosa* has been collected only on the walls of a shallow cave at 0.5 m depth and from a nearby shallow, shaded vertical rock wall and a wave-exposed rock outcrop near the Cabo Rojo lighthouse.

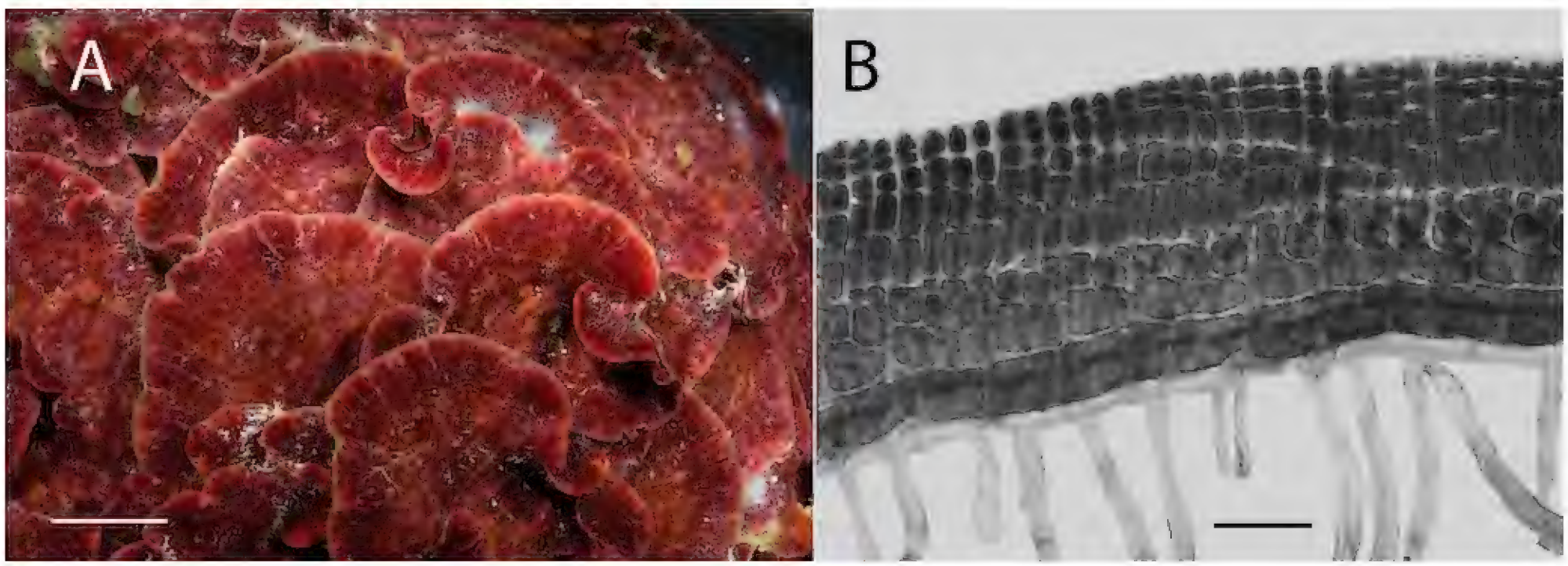

FIGURE 129. *Peyssonnelia stratosa*. (A) DLB8400, habit of preserved specimen, wave-exposed rock outcrop, Cabo Rojo lighthouse, 0.5 m. Scale bar = 1.0 cm. (B) Photomicrograph, radial transverse section. Scale bar = 50 µm.

Peyssonnelia tenuicrusta D.L.Ballant. et H.Ruiz sp. nov.

FIGURE 130

Peyssonnelia tenuicrusta D.L.Ballant. et H.Ruiz sp. nov., Fig. 130A–D.

Holotype: DLB8032 (U.S. Algal Coll. 328559), S.E. Mona Island, Coll. HR et al. (University of Puerto Rico technical divers), 70 m, 13.i.2010.

Paratype: DLB7519 (U.S. Algal Coll. 328561), edge of insular shelf ("Weinberg"), Coll. HR, 60.5 m, 3.vi.2003.

West Atlantic Distribution: Puerto Rico.

Etymology: The species name, *tenuicrusta*, means "thin crust" in Latin.

Description: Crustose thalli are closely adherent to their calcareous substrata and may spread to more than 8.0 cm in extent. Thalli (Figure 130A) are of variable thickness, ranging from 3 cells and 50 µm thick to 7 cells and 125 µm thick. Hypothallus cells are square to rectangular in shape, measuring 23–35 µm long and averaging 23 µm high. Shallowly boot-shaped coxal cells completely cover the hypothallial cells and average 13 µm high. Coxal cells cut off 2 files of ascending perithallial cells. Proximal perithallial cells average 20 µm long and 13 µm diam. Perithallial filament cells decrease only slightly in diameter distally. Terminal cells of the perithallial filaments are broadly obtuse. The hypothallus filaments, when viewed from beneath (Figure 130C), are arranged in parallel rows, and adjacent hypothallial cells are staggered. Short rhizoids, to 30 µm long, are cut off from the anterior ends of hypothallial cells. Tetrasporangial nemathecia are superficial, 600 µm in extent and to 200 µm tall, and unusual in that they appear to be corticated when developing (Figure 130D). This is due to terminal cells of the nemathecial filaments being enlarged and laterally coherent. Cruciately divided tetrasporangia measure to 110 µm long and 75 µm wide. Crusts are reddish orange in color.

Habitat and Comments: The new species is known only from deepwater habitats. In the absence of molecular data, the

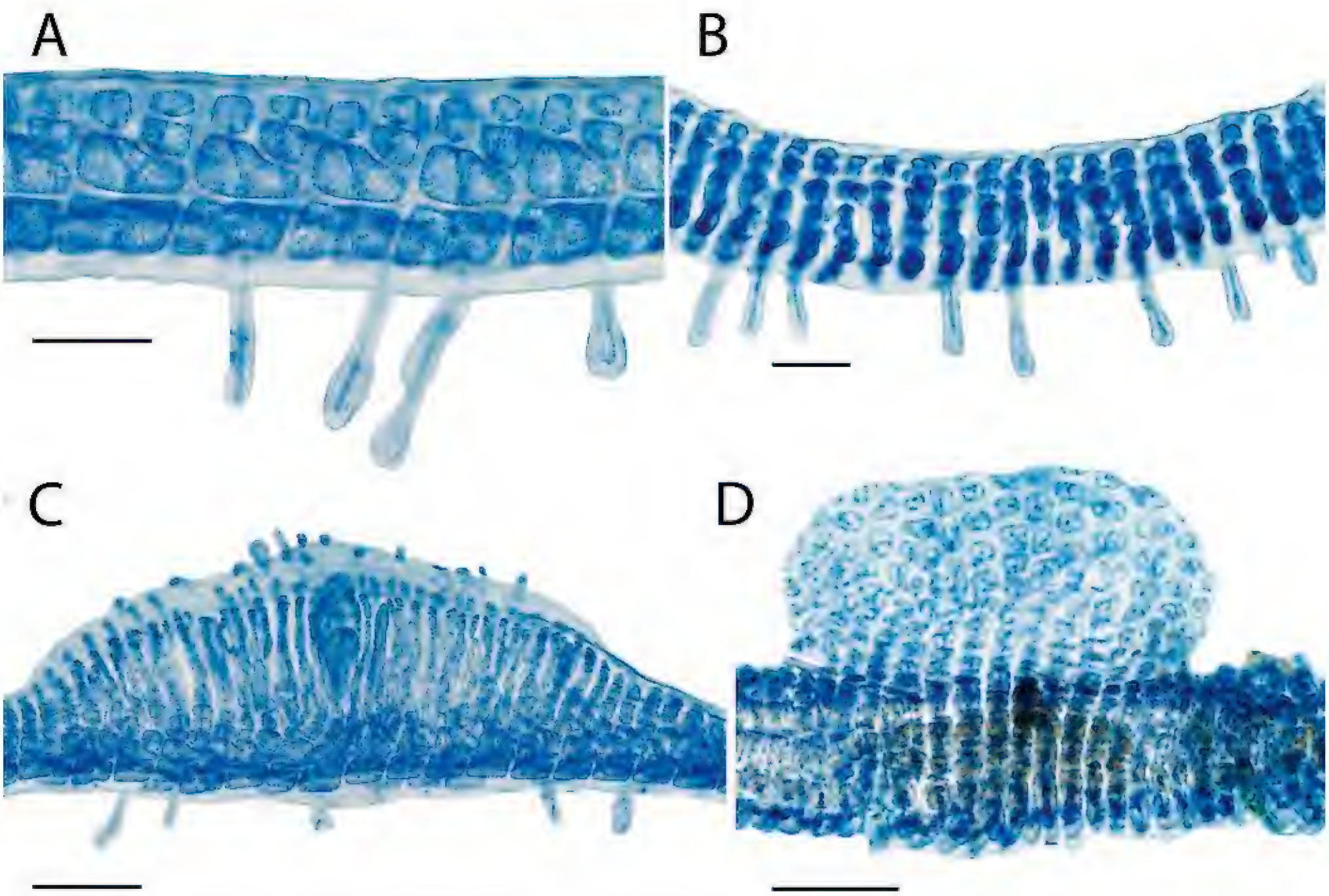

FIGURE 130. *Peyssonnelia tenuicrusta*. DLB8032, holotype. (A) Radial transverse section. Scale bar = 50 µm. (B) Tangential section. Scale bar = 100 µm. (C) Radial transverse section through tetrasporangial nemathecium. Scale bar = 100 µm. (D) Tangential section of tetrasporangial nemathecium with expanded terminal cells of the nemathecial paraphyses. Scale bar = 100 µm.

generic placement cannot be assigned with certainty among the somewhat morphologically similar thin-crust species of *Peyssonnelia*; *Agissea* Pestana, Lyra, Cassano et J.M.C.Nunes (2021); and *Olokunia* Pestana, Lyra, Cassano et J.M.C.Nunes (2021). Among the new genera, *Agissea* and *Olokunia* include species with unicellular rhizoids and a parallel arrangement of hypothallial cells when viewed ventrally. These species include *Agissea amadoi* Pestana, Lyra, Cassano et J.M.C.Nunes (2021: 7); *A. inamoena*; *A. simulans* (Weber Bosse) Pestana, Lyra, Cassano et J.M.C.Nunes (2021: 9); *A. stoechas* (Boudour. et Denizot) Pestana, Lyra, Cassano et J.M.C.Nunes (2021: 9); *A. taberniforma* Pestana, Lyra, Cassano et J.M.C.Nunes (2021: 1757: 9); *A. yemonjasagbae* Pestana, Lyra, Cassano et J.M.C.Nunes (2021: 10); and *Olokunia boudouresquei* (Yonesh.) Pestana, Lyra, Cassano et J.M.C.Nunes (2021: 13).

All differ from the new species in having substantially smaller tetrasporangia, less than 110 µm long and 75 µm wide. They additionally differ as follows: *Agissea amadoi* Pestana, Lyra, Cassano et J.M.C.Nunes (2021: 1755) possesses a poorly adherent crust, and there is apparently no overlap of adjacent hypothallial cells in ventral view. *Agissea inamoena* possesses a thicker crust (Schneider and Reading 1987); *A. simulans* has a thicker crust and tetrasporangia in immersed nemathecia. *Agissea stoechas* is loosely affixed to the subtratum and possess rhizoids greater than 125 µm long; *A. taberniforma* possesses substantially smaller tetrasporangia. *Agissea yemonjasagbae* is poorly adhered to the substratum, and the proximal periaxial cell is flattened. *Olokunia boudouresquei* possesses smaller tetrasporangia in immersed nemathecia (Schneider and Reading 1987); *Peyssonnelia conchicola* Picc. et Grunow in Piccone (1884: 317) also possesses tetrasporangia in immersed nemathecia.

Excluded Taxon

***Peyssonnelia rosenvingei* F.Schmitz in Rosenvinge 1893: 782, fig. 8.**

The Puerto Rican record is based on Díaz-Piferrer's (1963) report from wave-exposed habitats in Cabo Rojo and Ballena Bay, Guánica. The type locality of *P. rosenvingei* is Greenland, and Kato and Masuda (2000) regard the species to be of cold-water affinity. Dawes and Mathieson (2008) also regarded the presence of the species in Florida to be questionable. Furthermore, the accounts of vegetative morphology of the species by Taylor (1960) and Dawes and Mathieson (2008) are in considerable disagreement with that provided by Kato and Masuda (2000). We also regard the Puerto Rican record as being questionable.

Polystrata Heydr.

Polystrata Heydr. 1905: 35: pl. I.

Crustose thalli are completely calcified and closely adherent across the entire ventral surface and do not produce rhizoids. Thalli are composed of a monostromatic mesothallus that cuts off both dorsally and ventrally oriented filaments to form dorsal and ventral perithalli. The dorsal perithallus may or may not possess cell fusions and hair cells. Reproductive bodies are located in nemathecia. Gametophytes are monoecious. Three-celled carpogonial branches and 4-celled auxiliary cell branches are borne laterally on proximal cells of the paraphyses. Carposporangia are in simple chains of 2 or 3. Tetrasporangia are decussate or cruciately divided. One of the five *Polystrata* species recognized worldwide occurs in Puerto Rico.

Polystrata fosliei (Weber Bosse) Denizot

FIGURE 131

Polystrata fosliei (Weber Bosse) Denizot 1968: 161, 320, figs. 146–151.

Basionym: *Ethelia fosliei* Weber Bosse 1921: 298, fig. 108.

Puerto Rican Records: As *Polystrata fosliei*: Ballantine et al. 2011, 2016b.

Western Atlantic Distribution: Puerto Rico, Haiti, Colombia.

World Distribution: See Guiry and Guiry 2024.

Type Locality: Northeast point of Timor, Indonesia.

Thalli typically consist of many crust layers, measuring to 1.0–2.0 cm in thickness. Individual crusts, 125–365 mm thick, possess a mesothallus composed of cells 15– 40 µm diam. and 35–50 µm long. Obliquely ascending superior perithallial filaments measure 5.0–23 µm long and are 9–12 cells long. The proximal cell or the cell distal to it of the superior perithallus gives rise to 2 branched filaments. The inferior perithallial filaments are 6 to 8 cells long, and the cells measure 9.0–36 µm long. Superficial tetrasporangial nemathecia are oval in surface view, to 1.8 mm long, and are 160–200 µm high. Cruciately divided tetrasporangia are produced terminally on superior perithallial filaments and possess a unicellular pedicel. The tetrasporangia are ellipsoidal, measuring 90–110 µm diam. and 140–170 µm long. The simple paraphyses are 9–11 cells long. Algae are bright rose red in color.

Habitat and Comments: *Polystrata fosliei* is reported for Puerto Rico from both deep (to 70 m) and intermediate (17 m) depths (Ballantine et al. 2011). *Polystrata fosliei* is separated from the Papua New Guinea generitype, *P. dura* Heydr. (1905), in having superior and inferior perithalli of equal development as opposed to a poorly developed perithallium in the latter (Kato et al. 2006). Puerto Rican specimens consist of only single-layered thalli. [Additional illustrations Kato et al. 2006: figs. 1c, 4.]

Ramicrusta D.R.Zhang et J.H.Zhou

Ramicrusta D.R.Zhang et J.H.Zhou 1981: 538, 543, fig. 1, pls. I–II.

Thalli consist of calcified crusts that are either totally adherent to the substratum or partially free. Structurally, thalli possess a filamentous hypothallus that runs parallel to the substratum and a dorsal perithallus. Adjacent perithallial cells, particularly those in the lower perithallus, produce secondary pit connections that may or may not be accompanied by cell fusions and

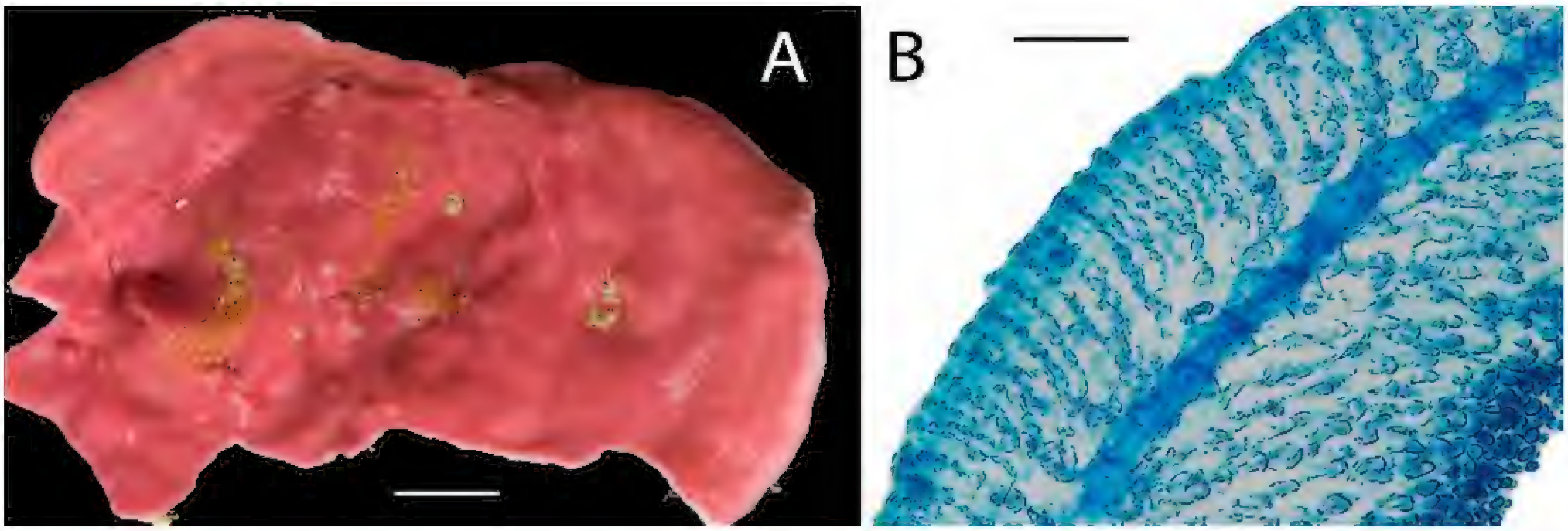

FIGURE 131. *Polystrata fosliei*. DLB7791. (A) Preserved specimen, 1.5 km seaward Media Luna Reef, 17 m. Scale bar = 0.5 cm. (B) Photomicrograph, radial transverse section. Scale bar = 100 µm.

horizontally oriented filaments. Hairs are present or absent in the distal perithallus. Rhizoids are unicellular. Gametophytes are presumably dioecious. Female nemathecia are superficial and made up of unbranched paraphyses. Two-celled carpogonial branches and 3- or 4-celled auxiliary cell branches are borne laterally on the proximal cells of paraphyses. Male and female gametophytes produce inconspicuous or elevated nemathecia. Tetrasporangial nemathecia are superficial, possessing unbranched paraphyses, with decussate or cruciately divided tetrasporangia that are cut off laterally on proximal paraphysal cells. There are 3 *Ramicrusta* species in Puerto Rico; 11 species of the genus are recognized worldwide.

KEY TO THE *RAMICRUSTA* SPECIES OF PUERTO RICO

1. Crusts are marginally free, possessing fluted or flared foliar extensions . . . . . ***R. textilis***
   Crusts are totally adherent to the substratum. 2
2. Thalli with superposed crusts dorsally . . . . . ***R. monensis***
   Thalli lacking superposed crusts. . . . . ***R. bonairensis***

***Ramicrusta bonairensis* D.L.Ballant., Lozada-Troche, H.Ruiz et J.N.Norris**

FIGURE 132

Ramicrusta bonairensis D.L.Ballant., Lozada-Troche, H.Ruiz et J.N.Norris 2016a: 425, figs. 18–21.

Puerto Rican Records: Ballantine et al. 2016a.

Western Atlantic Distribution: Puerto Rico, Netherlands Antilles.

Type Locality: Lac Bay, Bonaire.

Thalli are tightly adherent crusts with small rounded surface outgrowths. Crusts are thick, up to 840 µm (more commonly 400–670 µm) in thickness. Hypothallial cells appear to be arranged in parallel rows when viewed from the ventral surface. Rhizoids, infrequently produced, are unicellular and up to 170 (320) µm in length and 7.0–16 µm diam. Hypothallial cells, 35–45 µm in length and up to 40 µm high, give rise to assurgent perithallial filaments that are cut off singly from the center of the cell. Coxal cells are oval, 30–45 µm broad and up to 45 µm high.

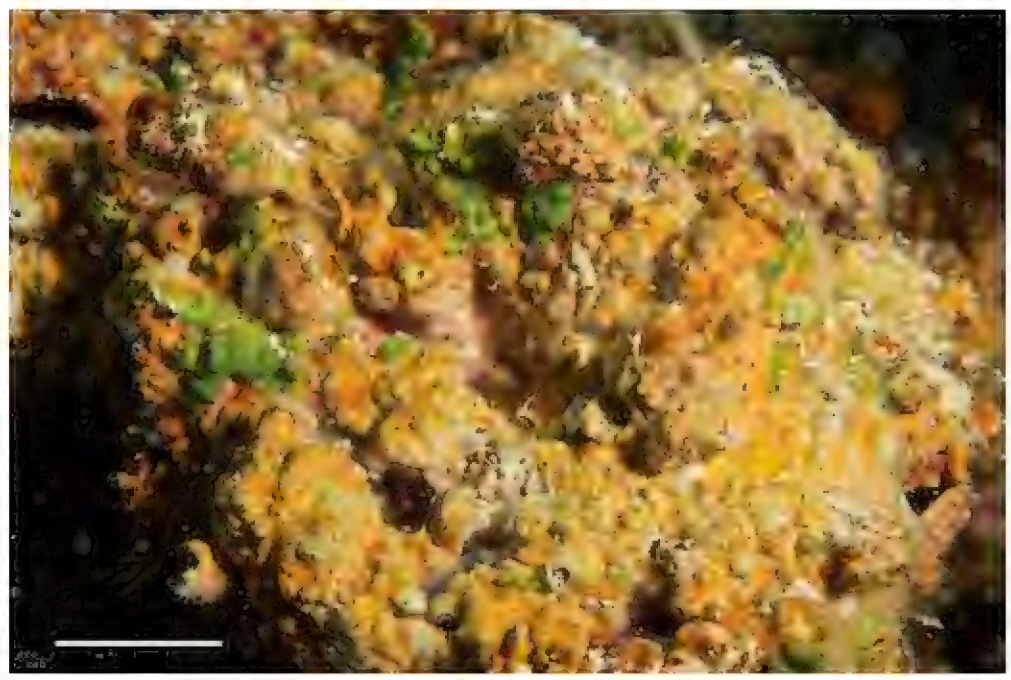

FIGURE 132. *Ramicrusta bonairensis*. DLB8481, field photograph, Cabo Rojo Lighthouse, 1.0 m. Field is approximately 10 cm.

Cells of the lower perithallus are also oval, becoming rounded above and appearing constricted at their bases. Perithallial cells of the lower perithallus are commonly pit connected to adjacent perithallial cells and occasionally are fused or possess lateral projections. There is a sharp discontinuity at the mid perithallus where cells rapidly decrease in size, with distal perithallial cells 15–20 µm broad and 15–20 µm high. Perithallial cells above the mid-perithallus discontinuity stain more darkly than those below, which enhances the layered appearance in stained sections. Upper perithallial cells are commonly pit connected to adjacent cells, and fusions are common. Hair basal cells or trichocytes are absent. Female nemathecia, greater than 2 mm in extent, are elevated to 225 µm above the perithallial surface. Carposporangia, 48 µm wide and 70–82 µm long, occur in files of 2–4 cells. Tetrasporophytes are unknown. Algae are bright orange to burgundy in color.

Habitat and Comments: *Ramicrusta bonairensis* overgrows a variety of scleractinian coral species in shallow water. The species was originally collected in Bonaire, Netherlands Antilles. In Puerto Rico it is known from a single specimen collected on rock outcrops in the vicinity of the Cabo Rojo lighthouse.

Ramicrusta monensis D.L.Ballant., H.Ruiz, Lozada-Troche et J.N.Norris

FIGURE 133

Ramicrusta monensis D.L.Ballant., H.Ruiz, Lozada-Troche et J.N.Norris 2016a: 421, figs. 8–17.

Puerto Rican Records: Ballantine et al. 2016a.

Western Atlantic Distribution: Puerto Rico.

Type Locality: Cocos Beach, Mona Island, Puerto Rico.

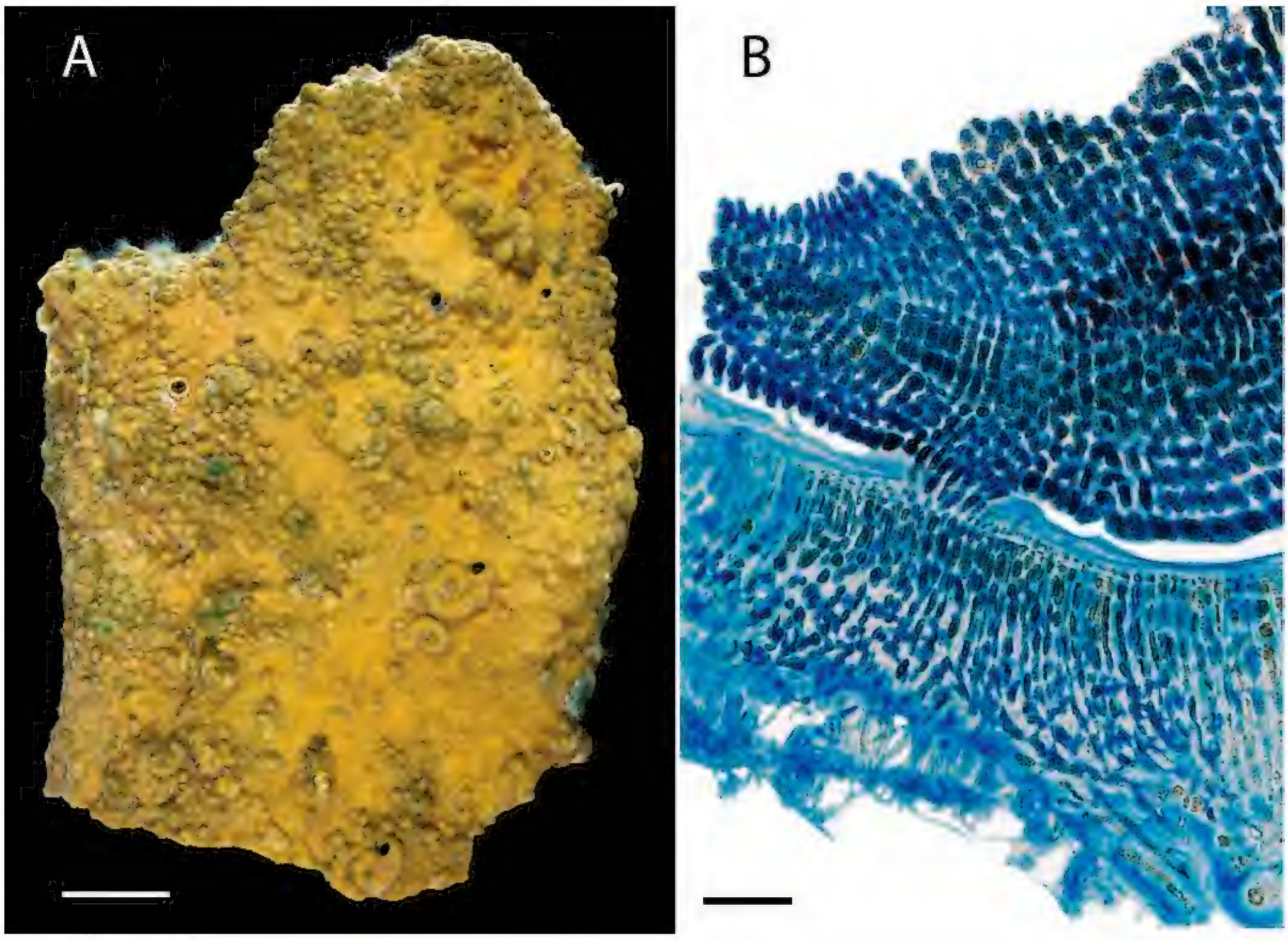

FIGURE 133. *Ramicrusta monensis*. DLB8360. (A) Preserved isotype specimen, Cocos Beach, Mona Island, 1.0–3.0 m. Scale bar = 1.0 cm. (B) Photomicrograph, radial transverse section, with tangential section of secondary crust overgrowing a lower crust. Scale bar = 100 µm.

Tightly adherent crusts, 585–650 µm thick, possess small rounded surface outgrowths. Thalli frequently form superposing crusts, commonly with a gap between the parent crust and the newly developed crust. Hypothallial filaments are arranged in parallel rows. Hypothallus cells produce short or elongate, unicellular rhizoids up to 200 µm long. Cells of the hypothallus are up to 35 µm long and 25 µm high. Assurgent perithallial filaments are cut off singly either from the center of a hypothallial cell or from its distal end. Coxal cells measure 13–20 µm diam. and 30–46 µm high. Thalli in section appear to be 2-layered due to an abrupt change in perithallial cell size distally as well as a difference in stain uptake. Secondary pit connections are present between adjacent cells of the upper perithallus but less common than below. Hair basal cells or trichocytes are present in the upper perithallus, measuring (10–)16–18 µm diam. and (10)20–23(–30) µm high. Male nemathecia are up to 85 µm high, with all of the nemathecial filament cells dividing to produce spermatangia. Female nemathecia are up to 200 µm tall above the perithallial surface. Auxiliary cell branches are cut off terminally from the basal cells of nemathecial filaments. Carposporangia are in occasionally branched files of 2–3 cells, measuring 50–70(–90) µm long and 25–30 µm diam. Nondivided tetrasporocytes, up to 80 µm long, are borne laterally on enlarged, cuplike, dark-staining basal paraphysal cells. Algae are yellowish in color.

Habitat and Comments: In Puerto Rico, *Ramicrusta monensis* is presently known only from 1.0–2.0 m depths at Mona Island, where it overgrows a variety of scleractinian coral species. Mixed reproductive phases with both male gametophytic structures and tetrasporangial nemathecia occurring on the same individual thalli have been observed.

Ramicrusta textilis Pueschel et G.W.Saunders

FIGURE 134

Ramicrusta textilis Pueschel et G.W.Saunders 2009: 481, figs. 1–20.
Puerto Rican Records: Ballantine et al. 2011, 2016a; Ballantine and Ruiz 2013; Williams and Garcia-Sais 2020.
Western Atlantic Distribution: Jamaica, Puerto Rico.
World Distribution: See Guiry and Guiry 2024.
Type Locality: St. Ann's Bay, Jamaica.

Individual colonies are up to 20 cm broad and equally high. The crustose thalli are rigid and brittle, with infrequent radial striations. Portions of thalli are adherent to the substratum, and foliaceous lobes sometimes form tubular vertical outgrowths with flaring margins. Calcification, heavy in hypobasal and proximal perithallial cell layers, decreases distally, and apicalmost cells may or may not be calcified. Hypothallial filaments are in parallel rows. The hypothallus cells are rectangular, measuring 30–60 µm long and 20–25 µm high. Unicellular rhizoids, 10–12 µm diam. and to 300 µm long, are cut off from the anterior ends of hypothallus cells. Lower cells of the ascending perithallial filaments commonly form pit connections with laterally adjacent cells, and fusions between adjacent cells are common. Apical and subapical cells of the perithallial filaments form a distinctive epithallial surface layer of small, 5.0–10 µm, cells, without cell fusions or secondary pit connections. Heterocysts are commonly present within the surface layer. Male gametophyte structures are inconspicuous, with spermatangia cut off singly or in 2-celled chains from apical perithallial cells. Female and tetrasporophytic structures occur in raised nemathecia. Auxiliary cells occur in 3-celled cell branches. Squarish or oblong carposporangia, up to 40 µm in largest dimension, are cut off

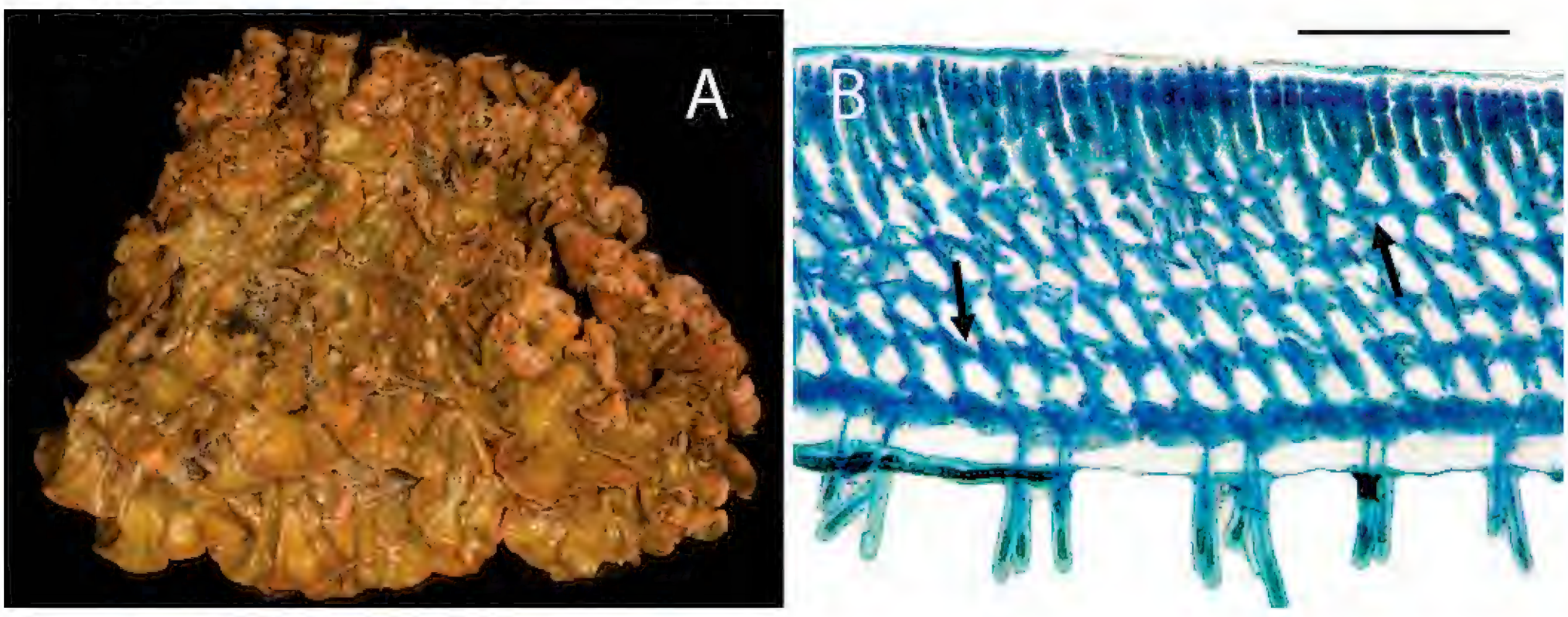

FIGURE 134. *Ramicrusta textilis*. DLB8416. (A) Habit of live specimen, east end, Caja de Muertos Island, Ponce, 1.0 m. Field is approximately 8.0 cm. (B) Photomicrograph, tangential section. Scale bar = 50 µm.

in chains of 2 or 3. Cruciately divided tetrasporangia, to 40 µm wide and to 90 µm long, are attached obliquely to the concave face of an asymmetrical, cup-shaped cell that may also bear a single cell or paraphysis terminally. Algae are golden brown in color and red brown where shaded.

Habitat and Comments: *Ramicrusta textilis* grows on rocks, coral rubble, and dead coral heads and commonly overgrows live coral in shallow, nearshore areas. Growth of the Puerto Rican *R. textilis* may be extensive and dominate their habitat (observed at Caja de Muertos, Ponce, in patches > 100 m^2). Williams and Garcia-Sais (2020) have documented a substantial and dramatic spread of the species in Puerto Rican coral reef habitats in recent years. [Additional illustrations: Ballantine and Ruiz 2013: figs. 1–3, supplementary video; Dixon and Saunders 2013: figs. 37–44; Ballantine et al. 2016a: figs. 1–3.]

Sebdeniales Withall et G.W.Saunders

Sebdeniaceae Kylin

Sebdenia (J.Agardh) Berthold

Sebdenia (J.Agardh) Berthold 1882: 530.

Thalli are multiaxial and composed of a filamentous medulla surrounded by pseudoparenchymatous cortical layers with cells decreasing in size toward the exterior. Secondary pit connections are present, and inner cells are multinucleate. Carpogonial branches are 3- or 4-celled, directed outwardly, and located on inner cortical cells. Auxiliary cells are intercalary in cortical filaments separate from those bearing carpogonial branches. Gonimoblast initials are single and oriented toward the thallus surface; the gonimoblasts form compact masses composed mostly of carposporangia. Cystocarps are deeply embedded. Tetrasporophytes are isomorphic with gametophytes and produce cruciately divided tetrasporangia scattered in the outer cortex. Thirteen *Sebdenia* species are recognized worldwide; one of these occurs in Puerto Rico.

Sebdenia flabellata (J.Agardh) P.G.Parkinson

FIGURE 135

Sebdenia flabellata (J.Agardh) P.G.Parkinson 1980: 12.

Basionym: *Isymenia flabellata* J.Agardh 1899: 66.

Heterotypic Synonym: *Halymenia agardhii* De Toni 1905: 1542.

Misapplied Names: *Sebdenia polydactyla* (Børgesen) M.S.Balakr. 1961: 89; *Halymenia elongata* C.Agardh 1822: 209.

Puerto Rican Records: As *Sebdenia polydactyla*: Ballantine and Norris 1989. As *Halymenia agardhii*: Almodóvar 1970; Almodóvar and Ballantine 1983; Ballantine et al. 1987. As *Sebdenia flabellata*: Ballantine and Aponte 1997a, 2002a. As *Halymenia elongata*: Ballantine and Aponte 1997a.

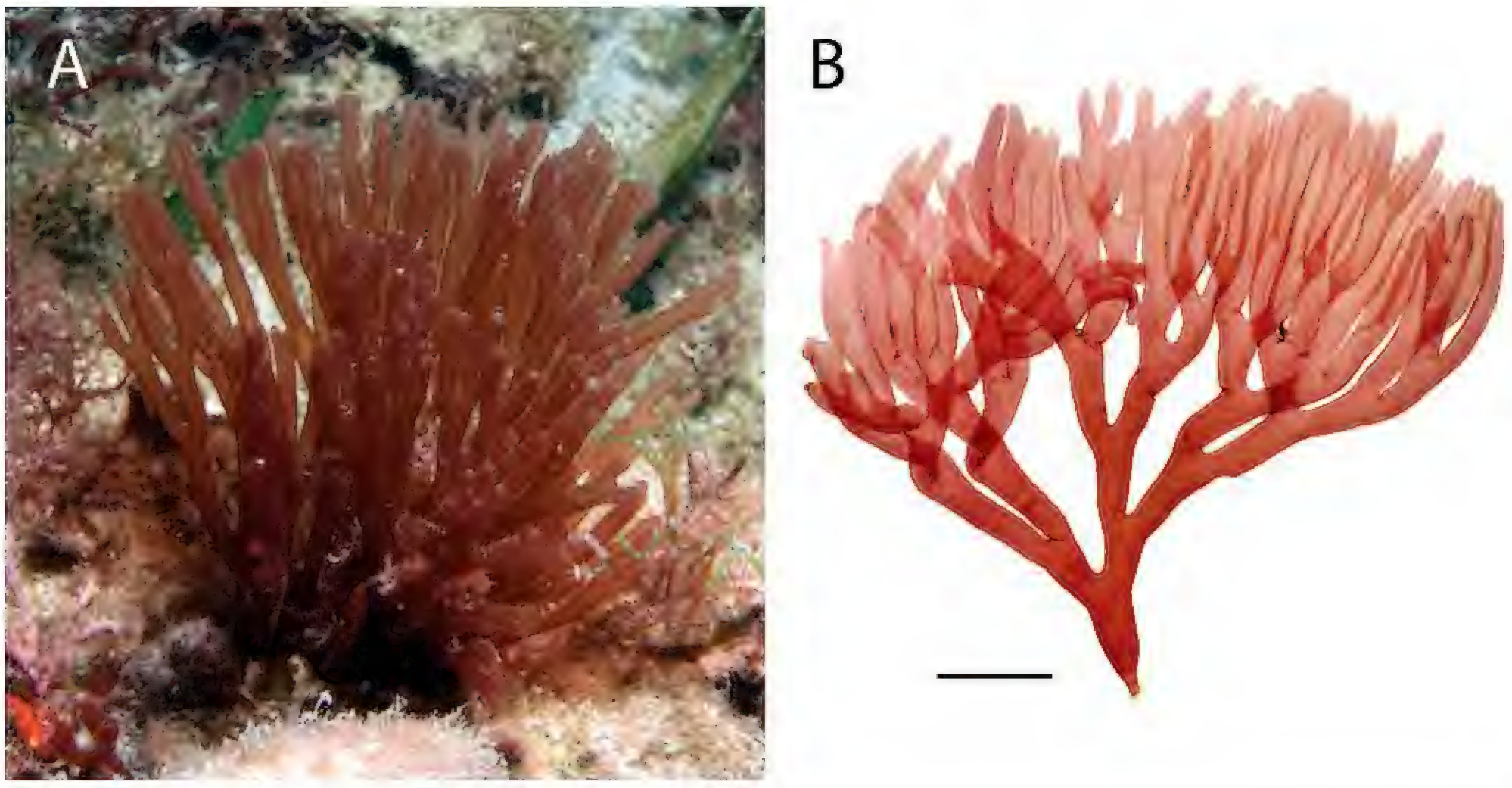

FIGURE 135. *Sebdenia flabellata*. (A) In situ habit photograph, algal plain, 1.5 km seaward Media Luna Reef, La Parguera, 17 m. Field is approximately 10 cm. (B) DLBsn, herbarium specimen. Scale bar = 1.0 cm.

Western Atlantic Distribution: Panama, Caribbean Mexico, United States (North Carolina, Georgia, Florida), Barbados, Bermuda, Guadeloupe, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2024.
Type Locality: Guadeloupe.

Lubricous thalli reach 4.0–30 cm in height. The cylindrical axes, 3.0–20 mm diam., are branched in a single plane and compressed below dichotomous branches. Axis apices are obtuse. The medulla is filamentous, with filaments measuring 3.0–10 mm diam.; gland cells and ganglia, 12–25 µm diam., are present. The cortex has 3–7 cell layers, with the outermost cells ovoid, measuring 3.0–9.0 µm diam. and 3.0–13 µm long. Pyriform spermatangia occur terminally on outer cortical cells. Three- to 4-celled carpogonial branches are borne on central cortical cells. Cystocarps, 150–300 µm diam., lack involucral filaments. Subspherical to irregular carposporangia measure 12–20 µm diam. Ovate tetrasporangia measure 13–27 µm diam. and 19–30 µm long. Algae are pink to deep red in color.

Habitat and Comments: *Sebdenia flabellata* has been commonly collected from the algal plain offshore from La Parguera at 17 m depth. [Additional illustrations: as *Halymenia agardhii*, Taylor 1960: pl. 51: fig. 1; Cordeiro-Marino 1978: figs. 146–148; as *Sebdenia flabellata*, Littler and Littler 2000: 109.]

Incertae Sedis

Hymenoclonium-Like

FIGURE 136
Hymenoclonium-like sensu Ballantine and Norris 1989: 6, figs. 2, 9, as *Hymenoclonium serpens* (P.Crouan et H.Crouan) Batters 1895: 319.
Puerto Rican Records: Ballantine and Norris 1989; Ballantine and Aponte 1997a; Ballantine et al. 2016b.
Western Atlantic Distribution: Puerto Rico.

Thalli grow as 1-cell-thick delicate skin-like encrustations made up of highly unordered networks of branched filaments. Cell aggregations of varying widths possess a central axis, composed of cells to 53 µm long. The axes cut off lateral cells of irregular shape and size to form segments, 15–70 µm wide. Branches are not typically initiated by the axial filaments; rather, a random lateral cell develops into a branch axis. Entire colonies reach to 5.0 mm in extent.

Habitat and Comments: The algal habit is very inconspicuous, observable only under magnification, and almost certainly has eluded previous and more recent recognition. In Puerto Rico the entity is occasionally found in water as shallow as 17 m depths but more commonly grows epiphytically and epizoically on various substrata at the edge of the insular shelf.

The genus *Hymenoclonium* was first documented from the tropical west Atlantic by Ballantine and Norris (1989) in reporting the entity from Puerto Rico as *Hymenoclonium serpens*. The basionym, *Callithamnion serpens* P.Crouan et H.Crouan (1858: 290, pl. 2: fig. 41–44, is initially known from Brest, France, at a depth of 20 m. The species is currently recognized as being a synonym of *Bonnemaisonia asparagoides* (Woodward) C.Agardh, as the tetrasporophytic life history alternate phase. Åsen (1980: 74) indicated that *B. asparagoides* "grows directly from *H. sperpens*." However, the inclusion of *Hymenoclonium* in *B. asparagoides* is regarded by Guiry and Guiry (2024) as "arbitrary," presumably indicating that they do not regard the association as specific.

There currently are only two members of the Bonnemaisoniales in the western Atlantic (Wynne 2011, 2022): *Asparagopsis taxiformis* (Delile) Trevisan, with a tetrasporophytic life history alternate that is well known to be the filamentous *Falkenbergia hillebrandii* (Bornet) Falkenb., and *Bonnemaisonia hamifera* Har. and its life history alternate *Trailliella intricata* Batters (1896). We consider it unlikely that "*Hymenoclonium serpens*" is associated with the life history of any west Atlantic alga.

Based on culture studies, other red algal species have been reported to have life history alternates with morphological

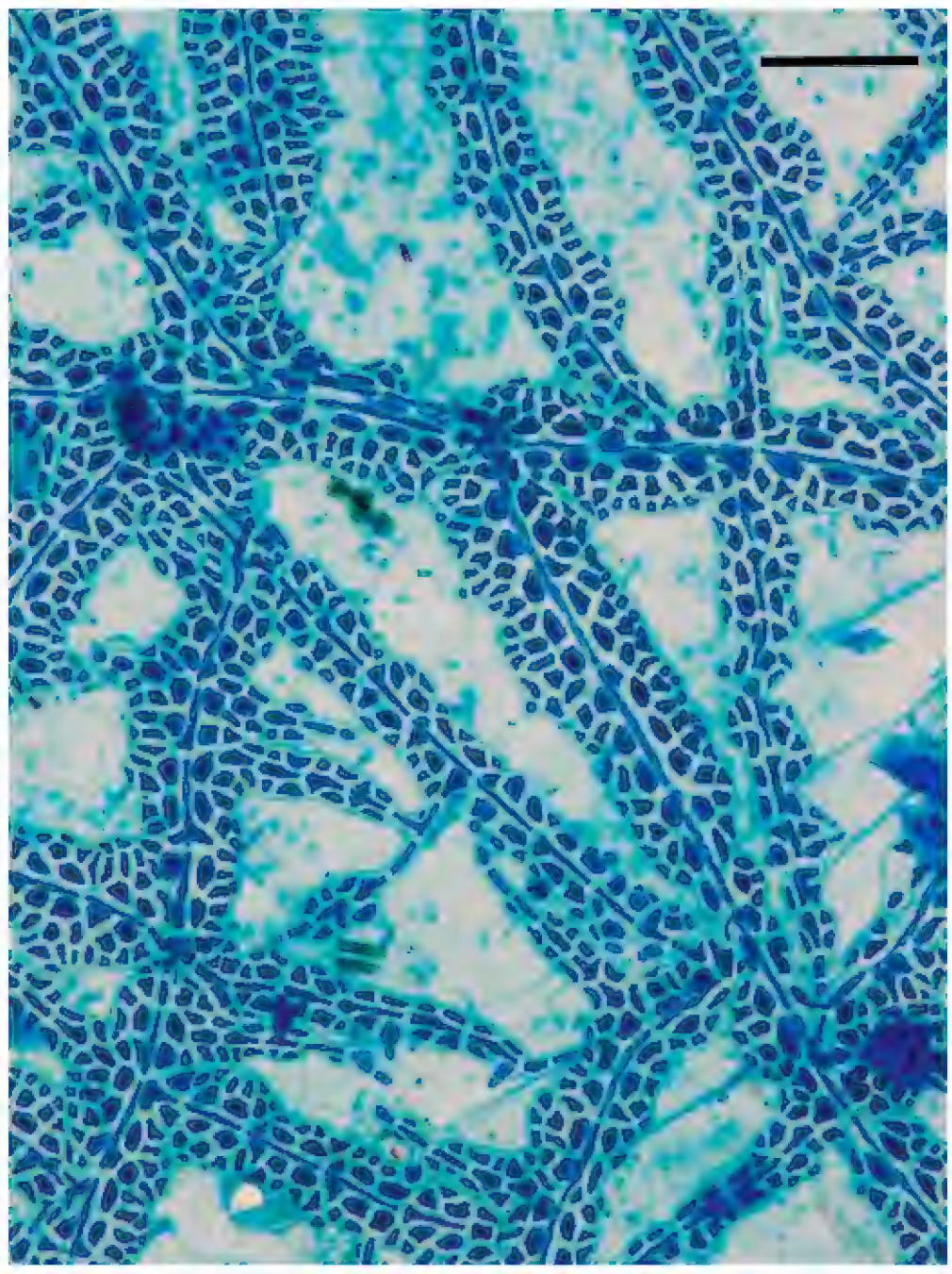

FIGURE 136. *Hymenoclonium*-like. DLB7453, edge of insular shelf, "Black Wall," 57 m, prostrate network of filaments. Scale bar = 50 µm.

similarity to "*Hymenoclonium serpens.*" These include the life history alternate of *Acrosymphyton purpuriferum* (J.Agardh) G.Sjöstedt. (see Cortel-Breeman 1975). Another morphologically similar tetrasporophytic life history alternate was reported by Guiry and Maggs (1984: figs. 11–23) for *M. microphylla* (J.Agardh) J.Agardh; they reported that carpospores germinated and formed a complex system of prostrate filaments resembling

Figure 134. *Meredithia* is represented in Puerto Rico by the deep-water species *M.? caribaea* and *M. pulchella*. Red algae with a "*Hymenoclonium*" growth habit are now recognized in both the Bonnemaisoniales and Gigartinales.

Nomenclaturally, "*Hymenoclonium serpens*" ceased to have taxonomic status when it was shown to be a life history alternate with another alga with nomenclatural priority (i.e., *Bonnemaisonia asparagoides*). For this reason, we consider that the name *Hymenoclonium* can be applied only as a form genus and this name undoubtedly applies to the life history stage of multiple species.

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Glossary

accessory Relating to a branch that is not in its expected location.

acute With a sharp point.

adaxial Toward the bearing axis.

adventitious Refers to structures, such as branches, that do not develop in an expected location.

allelopathy The effect on an individual by chemical products produced by another.

alternate As in branching, at different levels along an axis.

ampulla Arched filamentous systems that bear the female reproductive structures in the Halymeniales.

anastomose Secondary fusion of cells or branches.

annulate With ringlike cell wall ridges.

anticlinal Occurring at right angles to a surface or the circumference.

apiculate With a sharp point.

archeospore Asexual spores produced by Bangiophyceae.

arcuate Arching.

articulated Jointed.

assimilatory Refers to pigmented filaments.

assurgent Curving or growing upwardly.

attenuate Gradually narrowing.

auct. non Indication that subsequent authors have used a name in a different sense than that of the original author.

autonym An automatically created name of a subdivision under a validly published generic name in which its final epithet repeats the generic name unaltered.

auxiliary branch A branch that has an auxiliary cell.

auxiliary cell A reproductive cell in red algae that receives the diploid nucleus and gives rise to the carposporophyte.

axil Location that is immediately between an axis and a branch.

basiphyte An alga that is the host of an epiphyte or endophyte.

bifurcate Divided into two branches or projections of equal length.

bisporangia Sporangia with two meiotic division products.

bistratose With two cell layers.

bullate Puckered or blistered in appearance.

capitulum Head, such as a cluster of filaments that superficially resemble a head (pl. capitula).

carpogonium Egg cell or gamete produced by the female gametophyte.

carposporophyte The life history stage, composed of gonimoblast filaments, that is the result of germination of the fertilized carpogonium and that gives rise to sporangia by meiotic division.

carpotetrasporangia Sporangia produced by gonimoblast filaments as seen in Liagoraceae, in which there four carpotetrasporangia, presumably produced by meiosis.

cervicorn As in branching, in a manner similar to the antlers of a deer.

chromatophore Chloroplast.

clavate Club shaped, as an opening created by a fissure.

coaxial An anatomical arrangement of rows of cells that are aligned laterally in curving rows or are parallel to an axis (Guiry and Guiry 2024).

columella An axis of sterile tissue in the center of a reproductive conceptacle.

complanate In a single plane.

conceptacle Sunken or raised structure found in Corallinales in which reproductive bodies are located.

conchocelis Diploid microscopic filamentous life history stage of some Bangiales algae.

confluent Convergence of two or more parts.

connecting filament A tubelike structure that facilitates passage of the diploid nucleus from the carpogonium or fusion cell to one or more auxiliary cells.

conspecific Belonging to the same species.

cortex Outer layer of cells that have plastids, normally, cells to the exterior of the medulla.

corticated Possessing a cortex.

corymbose With the shape of a corymb; result of having branches arising at different points but terminating at the same level, giving the cluster a flat-topped appearance.

costa A longitudinally thickened rib.

coxal cell In Peyssonneliaceae, the proximal cell of the perithallus.

crenate With blunt or rounded teeth; scalloped.

crenulate Minutely scalloped.

crozier With respect to branch tips in *Hypnea musciformis*, a crozier tip is enlarged and incurved.

cruciate Appearance of the product of meiotic division in tetrasporangia, cross-shaped.

crustose Referring to a thallus that is adhered to a substratum.

cuneate Wedge-shaped, narrower end at the bottom.

cuticle Hyaline, polysaccharide outermost covering.

cystocarp The carposporophyte structure including the pericarp, if present.

cystolith A cell containing calcium carbonate.

daedaleoid Complex or intricate.

decumbent Growing in a prostrate manner, directly on the substratum.

decussate Situated successively at right angles. With respect to a sporangium, divisions form a cross.

dendroid Treelike branching.

dentate Toothed.

denuded Devoid of covering such as a lower algal portion lacking branches or branchlets.

determinate Of limited potential growth.

dichotomous As in branching, with two equal divergent branches.

digitate Branched with branching products spread from a common center, like fingers of a hand (see also palmate).

dimerous In sets of two; with respect to coralline red algae, there are two distinct groups of filaments that are oriented at right angles to each other.

dioecious Having male and female reproductive bodies in separate individuals.

distal Toward the apex of a thallus or structure, opposite of proximal.

distichous With branches arranged in opposite rows, thus in one plane.

distromatic With two cell layers.

dorsal At the rear or back; for an encrusting alga, dorsal would refer to the top surface.

dorsiventral A thallus that is organized into distinct dorsal and ventral surfaces.

ecorticate Without a corticating layer.

emarginate Possessing a notched margin.

endophyte A thallus that grows within the tissue of a host alga.

epidermis Outermost layer of cells.

epiphyte An alga attached to and growing directly on top of another alga.

epithallus Outer layer of a coralline red alga.
epitype An additional type for the purpose of clarification when the holotype may be ambiguous or otherwise insufficient.
epizoophyte An alga growing on an animal.
erose Having an irregularly notched or jagged margin.
excrescence Distinct outgrowth on an algal thallus.

farinaceous Gritty or mealy.
fascicle A cluster of filaments or branches from a single point.
fasciculate Branching in clusters.
fastigiate With branches that point upward; appearing parallel.
fide On the authority of.
filiform Very slender, filament-like.
fimbriate Fringed, having a margin with filiform processes.
flabellate Fan shaped.
flabellum Fan-shaped blade.
flagelliform Slender, elongated and flexible, like a whip.
flexuous Sinuous.
fruticose A thallus of non-articulated coralline algae with shrub-like branches.
furcate Forked, as in a terminal division.
fusiform Spindle-shaped; narrowing from the middle toward each end.
fusion cell An enlarged cell formed by fusion of the carpogonium or auxiliary cell with vegetative cells of the female gametophyte.

gametangia Structures in which gametes are formed.
gametophyte In life histories, the haploid generation.
ganglia Refers to ganglionic cells that have elongate processes.
generative auxiliary cell The cell that ultimately receives the diploidized nucleus from syngamy and gives rise to the sporophytic generation.
generitype The type species of a genus.
genicula The normally flexible, noncalcified joints between segments of articulated coralline algae.
gonimoblast A filament of diploid cells that comprise the carposporophyte.

hair mother cells As in non-geniculate red algae, a normally somewhat enlarged cell that gives rise to a hair cell.
haptera An attachment structure.
heterocyst Normally refers to a specialized structure in Cyanobacteria associated with nitrogen fixation. With respect to coralline algae, it is a differentiated, somewhat enlarged cell.
heteromorphic With respect to red algal life histories, the term refers to morphological differentiation between gametophyte and tetrasporophyte generations.
heterotrichous Having a thallus comprising both a prostrate and erect system.
holotype The single specimen on which the author of a new species bases the description.
hyaline Colorless or translucent.
hypobasal Underneath the hypothallus.
hypogynous cell The cell beneath the female carpogonium.
hypothallus Basal-most layer of cells.

imbricate Overlapping layers.
indeterminate Potential unlimited growth of an axis.
intergenicula In articulated coralline algae, the calcified segments.
indusium Membrane covering sporangia.
intercalary Located between the base and apex of a branch or filament.
interstitial Cells located within spaces between other cells.
involucre Sterile filaments that surround a reproductive structure.
isodiametric Cells or structures whose length and diameter are the same.
isomorphic With respect to red algal life histories, the term refers to morphological identity between gametophyte and tetrasporophyte generations.

jacket cell In *Naccaria*, jacket cells are enlarged cortical cells that surround the axis.

lacerate Ragged, as the margin of a blade.
laciniate Irregularly divided into deeply clefted lobes.
lacunate Possessing a cavity.
lanceolate Elongate, tapering distally.
lectotype Specimen chosen in the absence of a holotype.
lenticular Shaped like a lens. For example, in a case where a medullary cell has a partial enlargement of the cell wall, that cell in section appears lenslike.
linear Narrow with respect to length.

linear-oblong Elongate and not tapered.
lobate With lobes.
longitudinal Perpendicular to the long axis, as in a section.
lubricous Having a slippery or slimy quality.
mammillate Breast-like protuberances (mammilliform).
medulla Center of the thallus, beneath the cortex.
mesothallus A layer of cells, normally centrally positioned, that cuts off both ascending and descending perithallial filaments.
molariform Appearing like a molar tooth.
monoecious Having both male and female reproductive bodies on the same individual.
monomerous In non-geniculate Corallinales, thallus structure with a single pseudoparenchymatous system in which some derivatives are oriented parallel to the thallus surface and others curve outwardly (Huisman 2018).
monopodial Type of growth in which continuous growth occurs behind and apical cell and lateral branches remain subordinate.
monosiphonous Comprising a single filament.
monosporangia Sporangia that give rise to a single spore.
monospore A single asexual cell.
monostromatic Single cell thick.
monotypic A genus comprising a single species.
multiaxial Thallus construction by multiple filaments, recognizable at the apex by a cluster of apical cells.
multiseriate Comprising multiple filaments.
nemathecium A raised thallus portion with an aggregation of reproductive cells (pl. nemathecia).
nitent Glossy.
nutritive cell Associated with the auxiliary cell of some Rhodophyta, presumably contributing to nutrition of the developing carposporophyte.
oblanceolate See lanceolate; however, broadest in the upper third.
oblong Having a length several times greater than the width and with rounded ends.
obovate Egg-shaped, attached at narrower end.
obtuse Having a blunt or rounded end.
opposite With respect to branching, occurring on opposite sides of their common axis.
orbicular Flat, with a more or less circular outline.
orthostichous Refers to the arrangement of structures, such as branches, that are situated vertically along an axis, such that one is directly above the one below.
ovate Egg-shaped; attached at broader end.
palisade cells Columnar-shaped cells in non-geniculate coralline algae that occur in rows or tiers forming the outer cortex.
palmate Branching that radiates from a common point, as in fingers radiating from the palm of a hand.
paniculate A branched cluster.
papillae Small elongated protuberances.
paraphyses Normally uniseriate, sterile filaments lying between reproductive structures.
parenchyma Three-dimensional tissue formed by closely abutting cells.
parietal Internal and positioned against the periphery.
pectinate Closely set and unilaterally branched, like the teeth of a comb.
pedicel A stalk, normally one or a few cells.
pedicellate Possessing a pedicel.
peltate Shield-shaped, borne by a more or less centrally placed stalk.
percurrent Running through the entire length, as an axis that is distinct from base to apex.
pericarp A haploid structure in some red algae that surrounds the cystocarp.
peristome With respect to red algae, the peristome is the elongated neck of a carposporophyte.
perithallus Constituted by the erect growing filaments found in members of the Peyssonneliales.
pinnate Branches arranged on opposite sides of a common axis.
pit connection A result of incomplete cytokinesis when Florideophyceae red algal cells divide, appearing as thin threads between adjacent cells. Primary pit connections indicate relatedness between cells, and secondary pit connections may subsequently be formed.
plano-compressed Compressed with flat sides.

pluriseriate Having multiple lengthwise axial filaments.

polychotomous With numerous branches from a common branching point.

polygonal Many sided, with flat polyhedral faces.

polyhedral Three-dimensional shape in which there are multiple faces.

polymorphism Meaning many forms. Some algae change their appearance or morphology when growing under differing conditions.

polystromatic Many layers of cells.

proliferous Bearing abundant branches.

propagule A portion of an alga that can break off, leading to asexual reproduction.

pro parte In part; indicates that a taxon contains more than given entity.

proximal Toward the base of a thallus or structure, opposite of distal.

pseudodichotomous Appearing to be dichotomous, but not resulting from the equal division of an apical cell.

pseudofilament A linear series of cells held together by a gelatinous sheath, resembling a filamentous structure.

pseudoparenchyma Tissue resembling a parenchyma, but originating from the close association of axial filaments.

pulvinate Cushion shaped.

pyrenoid Structure within some plastids; site of starch synthesis.

pyriform Tear or pear shaped.

quadrate Four-sided, approximately square in shape.

quadripartite Divided into four parts.

radial With structures radiating from a central point.

radial transverse A section that is cut lengthwise along the growing axis.

reniform Kidney-shaped.

repent Growing flat on the substrata.

reticulate Netlike arrangement.

rhizine A thick-walled rhizoidal filament seen in some Gelidiales.

rhizoid Attachment, absorptive or corticating filament.

rhizomatous Possessing a below-sediment growing axis.

rhodolith Nonattached coralline red algal nodule that frequently forms when an encrusting coralline species envelops a stone or other object.

saxicolous Living or growing on rock.

secund Bearing branches produced from the same side of an axis.

sensu In the sense of.

seriate Arranged in rows.

sessile Immobile; attached without a stalk.

simple Unbranched.

sinus A recess between two structures; also used in reference to branching angle.

spathulate Expanded distally, like a spoon.

spermatangia Cells that produce spermatia.

spermatia Male gametes.

sporangia Structures in which spores are formed. For Rhodophyta species, sporangia are typically produced by sporophyte generations.

sporophyte Diploid generation in red algal life histories.

spur branchlet Short outgrowth.

squamulose Possessing small scales.

stellate Star-shaped; producing projecting arms from a usually enlarged cell.

stipe Stalk.

stipitate Bearing a stalk.

stolon A prostrate axis; see also rhizome.

subconical Nearly or almost conical.

subcortex Inner portion of the cortex.

subdichotomous As in branching, nearly or almost dichotomous.

superpose Superimposition.

support cell The cell on which the carpogonial branch is borne.

syntype One of several specimens mentioned in a species description in which the author did not designate a holotype.

terete Cylindrical.

tetrachotomous Refers to branching in which there are four branches from a branching node.

tetrahedral Type of division, at oblique angles, of tetrasporangia. Generally, three of the four meiotic products are visible.

tetrasporangium Sporangium that contains four spores produced by meiotic division.

tetraspore One of the four spores produced in a tetrasporangium.

textorii Refers to shallow spermatangial conceptacles in *Gracilaria*.

thallus The body of an alga (pl. thalli).

topotype A specimen of a species that was collected from the type locality.

trapezoid Refers to a shape in which one pair of opposite sides (of unequal length) is parallel.

trichocyte A structure in a Corallinales thallus that consists of a hair cell and one or two support cells.

trichotomous Refers to branching in which there are three branches from a branching node.

triphasic Refers to the life history type in some Florideophyceae in which there are three morphological entities: gametophyte, carposporophyte, and tetrasporophyte.

type A (usually herbarium) specimen on which the name of a taxon is based; see holotype.

type locality The geographical location where the holotype was collected.

uniaxial Possessing a single axial filament.

unilateral With branches produced from only one side of a bearing axis.

unilocular Referring to a reproductive organ bearing a single chamber.

uniseriate Having a single lengthwise axial filament.

unistratose Possessing a single layer.

ventral Pertaining to the lower surface; opposite of dorsal.

whorled A ring of branches or branchlets borne on the same level on an axis.

zonate Demonstrating banding.

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